COELACANTHS FROM THE
BEAR GULCH LIMESTONE (NAMURIAN)
OF MONTANA AND THE EVOLUTION
OF THE COELACANTHIFORMES

RICHARD LUND AND WENDY LAURIE LUND
*Biology Department, Adelphi University,
Garden City, New York 11530*

CONTENTS

ABSTRACT

The coelacanth *Rhabdoderma elegans,* type species of the family Rhabdodermatidae, is redescribed on the basis of material from the type locality at Linton, Ohio (Westphalian), other species assigned to the genus are discussed, and the rediagnosed family is assigned to the suborder Coelacanthoidei. The new genus *Dumfregia* is created for *Coelacanthus (=Rhabdoderma) huxleyi* Traquair from Glencartholm, Scotland (Visean). The osteology and ontogeny of *Caridosuctor populosum* (Rhabdodermatidae), *Hadronector donbairdi, Allenypterus montanus, Polyosteorhynchus*

simplex (family Hadronectoridae, suborder Hadronectoroidei), and *Lochmocercus aciculodontus* (suborder incertae sedis), from the Bear Gulch Limestones of Fergus County, Montana (Chesterian), are described. The Devonian genus *Diplocercides (=Nesides?)* is assigned to the Coelacanthoidei.

Character states among the Osteichthyes are evaluated, and the possible interrelationships of the Coelacanthoidei, Sarcopterygii, and Crossopterygii are discussed.

INTRODUCTION

The osteichthyan order Coelacanthiformes includes fish ranging in age from late Devonian to recent, which differ from each other only in proportions or relatively small details of osteology. Essentially unchanged and essentially similar in all aspects are the basic body shape and fin disposition, or locomotor system, and the basic head and mouth shape, or feeding system, of all but one species, *Allenypterus montanus* (Melton, 1969). The coelacanths, therefore, are the longest surviving group of virtually unchanged vertebrates known.

The fossil record of coelacanths includes both fresh and salt water forms through the Triassic, including deposits primarily of small individuals in the Visean of Glencartholm, the Westphalian of Braidwood, Illinois (Schultze, 1972), Cannelton, Pennsylvania, and Linton, Ohio, and upper Triassic Newark supergroup of the eastern United States (Olsen and Galton, 1977). While there is some question about the salinity of the Glencartholm coelacanth beds the remainder are fresh water (Richardson and Johnson, 1971; Schram, 1976; Olsen and Galton, 1977). The Braidwood coelacanths include a number of individuals with yolk-sacs (Schultze, 1972) indicating not only that ovoviviparity was established in this group by the Pennsylvanian (Smith et al., 1975), but

strengthening the suggestion that these deposits may have been spawning grounds (Thomson, 1969). Many other coelacanth-bearing deposits contain few, large specimens which have given an inadequate picture of the habitat and morphology of this group. The morphology and relationships of the Paleozoic Coelacanthiformes are particularly poorly known.

Coelacanths of five species represent approximately 15% of the fish specimens collected from the lower Carboniferous marine Bear Gulch Limestone of Montana (Lund, 1977). The fish fauna currently totals about 2,100 specimens and 76 species in four classes of which 41 species are chondrichthyan and 33 osteichthyan. One of the coelacanth species *Caridosuctor populosum,* is by far the most abundant fish in the fauna. A size and growth range can be demonstrated for three of the five species which indicates growth from birth to maturity occurred within the confines of the basin.

The ecomorphology of the Bear Gulch coelacanths has been discussed elsewhere (Lund et al., in press). This paper is limited to a consideration of their morphology and relationships and other Paleozoic coelacanths are considered in detail where this is needed to clarify these questions.

MATERIALS AND METHODS

Specimens occur in a variety of lithologies which are sequentially repeated at about 3 ft intervals throughout the 35 ft of productive limy silts quarried in the Bear Gulch member (Horner and Lund, in press). There are no detectable faunal differences in this stratigraphic interval (Scott, 1973).

The repetitive units range from a massive, extremely well indurated fine grained grey silty limestone which may laterally grade locally into beds of good fissility, downward through slight-

ly coarser, less limy yellowish stone into a poorly indurated zone of soft, fine, pink to brown, thin bedded, irregularly fissile material best described as siltstone. One or more thin pure white caminace of non-indurated material frequently can be found at or near the base of the faule material, which is succeeded below by the next massive zone. Deposition is comparable to the lithographic limestone deposits of Bavaria (Williams, 1981).

Specimens occurring in the softer lithologies may readily be

prepared by the use of needles and photographed with standard techniques. Specimens from the dense grey layers lend themselves to the removal of all bone from the head with needles and the preparation of impressions with latex (Baird, 1955). Contrast enhancement photography, using Kodak high contrast copy film at an ASA rating of 32 and three successively slower exposure times, combined with Ethol T.E.C. developer diluted 1:15 at the film's recommended developing times produced outstanding results. A blue (Wrattan 82A or equivalent) filter was also found helpful in contrast enhancement. All line drawings were prepared from a photographic base. The terminology of the skull bones follows Andrews' (1973) rhipidistian terminology wherever possible.

Specimens are deposited in the University of Montana fossil verebrate collections (MV) or the Section of Vertebrate Fossils, Carnegie Museum of Natural History (CM). Specimens have been referred to from the Royal Scottish Museum (RSM), Edinburgh, Scotland, and the Hancock Museum (HM), Newcastle, England.

SYSTEMATICS

Introduction

The Coelacanthiformes are included within the Crossopterygii on the basis of the common possession of two dorsal fins, lobed paired fins, and an intracranial joint dividing the braincase into anterior and posterior (ethmosphenoid and oticooccipital) parts. Coelacanths also share with many crossopterygians the possession of cycloid scales, a diphycercal tail, and a hyomandibula, which is not firmly held to the palate, but does aid in palatal suspension (Andrews, 1973; Jarvik, 1954). Coelacanths differ from other crossopterygians in lacking cosmine, lacking a maxilla, having a small dentary and large angular in the lower jaw, as well as in other details summarized in Table 8. While details of the interrelationship of the Coelacanthiformes with other crossopterygians are vague, only Miles (1977) in recent years has questioned the basic interrelationships. Evidence bearing on this question will be discussed further in this paper in light of the coelacanths described below, but there is no convincing evidence on which to base removal of the Coelacanthiformes from the Crossopterygii.

The Subordinal Question

The order Coelacanthiformes derives its name from the first described species, *Coelacanthus granulatus* Agassiz, from the Permian Marl Slate of Durham and Northumberland, England (Agassiz, 1837; Moy-Thomas and Westoll, 1935). Three suborders have been named, the Diplocercidoidei, Coelacanthoidei, and the Laugioidei (Obruchev, 1967). The suborders are based principally on chronology, with all Devonian and Carboniferous coelacanths except the Carboniferous *Coelacanthus* species being included in the diplocercidoids. All post-Carboniferous coelacanths except *Laugia* (Stensiö, 1921) are

considered coelacanthidoids (Obruchev, 1967). *Laugia* has been placed in its own suborder solely on the basis of a pelvic girdle modified for attachment to the pectoral girdles. This character complex alone hardly has the morphologic, functional, or phylogenetic level of significance which normally would accompany subordinal separation (Greenwood et al., 1966).

Two families have been included in the Diplocercidoidei, the Devonian Diplocercidae (Stensiö, 1937) and the Carboniferous Rhabdodermatidae (Berg, 1958). The major subordinal criteria have been: a solidly ossified braincase versus reduced braincase ossifications; presence or absence of a suboperculum; presence of a basipterygoid process; size of the ectopterygoid and the size of the vomers. Only *Diplocercides* of the Diplocercidae possesses a solid braincase and a basipterygoid process (Stensiö, 1937; Bjerring, 1973), rendering these characters useful at the generic level if at all. As discussed below, the elements which have been called the suboperculum and preoperculum in coelacanth literature (Schaeffer, 1952) are actually homologous to the preoperculum and quadratojugal, respectively, of crossopterygians (Andrews, 1973). No coelacanths described prior to the Bear Gulch forms have a suboperculum and the character as previously used is incorrect. The size, or even the presence, of the ectopterygoids and vomers cannot be satisfactorily demonstrated in many coelacanths, and the contention that large vomers are primitive (Obruchev, 1967) is contradicted by Andrews (1973). Neither character seems to be consistent or useful at any taxonomic level higher than genus. To summarize, prior to the introduction of the new evidence in this paper, the criteria for coelacanth suborders are either significant at the generic level only, trivial, or incorrect. The suborders previously proposed have no taxonomic applicability.

PALEOZOIC TAXA OF FAMILY RANK

The Diplocercidae, Rhabdodermatidae and Coelacanthidae have been named in reference to *Diplocercides kayseri* from the Devonian (Stensiö, 1922), *Rhabdoderma elegans* from the Pennsylvanian (Berg, 1958), and *Coelacanthus granulatus* from the Permian (Agassiz, 1839), respectively. *Coelacanthus granulatus* typifies the problems which have existed among coelacanths. Morphological information on the type species of the type genus, and therefore the lynchpin of coelacanth studies, was limited to the posterior dermal cranium and postcranial skeleton (Moy-Thomas and Westoll, 1935) until Schaumberg's revision in 1978. The cranial information, which follows, is taken from Schaumberg (1978), the postcranial from Moy-Thomas and Westoll (1935).

The premaxillae consist of several splint-like tooth plates, and bones of the rostral area are small, numerous and loosely associated, hence poorly known. The skull roof of the ethmosphenoid region has a large postrostral flanked by three or four paired frontonasals, followed by a pair of parietals; the skull roof itself is flanked by a single series of supraorbital canal bones. The infraorbital canal bones consist of a large lateral rostral, a lacrimojugal and a postorbital, but an antorbital is lacking. There are three bones in the cheek, an isolated quadratojugal, and a squamosal and preoperculum reduced to lateral line canal tubes. A suboperculum is lacking.

The skull roof of the otico-occipital consists of long postparietals and posterolateral tabulars, followed by a small posttemporal and seven extrascapulars along the posterior edge. The supraorbital lateral line is restored as joining the infraorbital canal at the lateral rostral anteriorly and the otic canal in the postparietal posteriorly.

The shoulder girdle contains an anteriorly directed, triangular supracleithrum, large cleithrum, laterally overlapping extracleithrum, and clavicle. The pelvic plate sutures to the contralateral element via a posterior, mesially directed process, articulates with the fin axis via a posterolateral expansion and bears a thin anteromesial lamina strengthened by two ridges. The anal plate is simple, and lies parallel to the body wall midway between pelvic and anal fins. The first dorsal fin plate is rounded above, with a straight lower edge, while the second dorsal plate resembles a posteriorly reclining T, the lower limb of which rests in a notch formed by several shortened neural spines. There is a one-to-one relation-
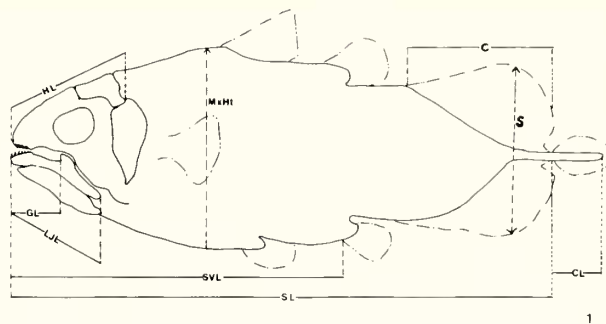

Fig. 1.—Measurements. Abbreviations: C, chord; CL, length of caudal lobe; GL, gape length; HL, head length; LJL, lower jaw length; MxHt, maximum height; S, span (aspect ratio of tail = span/chord); SL, standard length; SVL, snout–vent length.

ship between the caudal fin rays and their endoskeletal supports. There are bony ribs.

Schaumberg concludes (1978) that *Latimeria* is sufficiently close to *C. granulatus* that they both belong in the family Coelacanthidae. While there are difficulties in accepting Schaumberg's restoration of the ends of the supraorbital canal, for reasons elaborated on in the subsequent discussion, our analysis completely agrees with his conclusions.

All Permian and Mesozoic coelacanths have previously been included in the family Coelacanthidae except *Laugia* (Berg, 1958; Obruchev, 1967; Romer, 1966), the Laugiidae being distinguished on the basis of its unique pelvic girdle. As considerable cranial information exists on Mesozoic coelacanths (Schaeffer, 1952, 1967), the new diagnosis of *C. granulatus* now permits a revision of the Mesozoic coelacanths as well as an attempt to analyze and compare the other nominal coelacanth families.

The family Rhabdodermatidae has had a checkered history. J. S. Newberry (1856, 1873) described three species of coelacanths, *Coelacanthus elegans, C. ornatus* and *C. robustus,* from the cannel shale below the Upper Freeport Coal, late Westphalian D, of the Linton mine, Jefferson County, Ohio. *C. elegans* was distinguished from *C. ornatus* by finer vermiform scale ornamentation. *C. robustus,* known only from fragmentary large specimens, was suggested to be the adult of *C. elegans* by Newberry (1873).

The genus *Rhabdoderma* was erected by Reis (1888), *C. elegans* being designated the type species. Moy-Thomas (1937) placed *R. ornatus* and *R. robustus,* as well as several other coelacanths from the American and European late Carboniferous into

synonymy with *R. elegans* on the basis of scale or-namentation and fin plates. Moy-Thomas presented a revised description of the species, with a resto-ration (Moy-Thomas, 1937, fig. 1) which is devoid of reference to the horizons, localities, or specimen numbers used in its construction. This is the only nearly complete restoration of a Carboniferous coel-acanth in print and has served as the basis for the family Rhabdodermatidae of Berg (1958) as well as all subsequent attempts to analyze the evolution of the Coelacanthiformes (Schaeffer, 1952; Echols, 1963; Obruchev, 1967; Andrews, 1973).

Over 135 acid cleaned and latex peeled *Rhab-doderma* have been prepared from specimens col-lected by my field parties at Linton, Ohio. These specimens, now in the collection of Carnegie Mu-seum of Natural History, Pittsburgh, range in size from a complete individual of 49 mm total length to a poor skull of a fish of estimated 321.6 mm total length. It is clear from analysis of the specimens that there is only one species, *R. elegans,* in the Linton deposits. It is also clear that *R. elegans* is not the species described and illustrated by Moy-Thomas (1937).

Having synonymized a number of nominal species with *R. elegans* principally on the basis of orna-mentation, Moy-Thomas (1937) incorporated the remainder of the British Carboniferous species into the genus and named four new species on the same basis, from few isolated bones. One species, *Coel-acanthopsis curta* Traquair (1905), however, was considered "indeterminable" by Moy-Thomas. Reexamination of the type and only known speci-men of *Coelacanthopsis curta* by the authors does not clarify the osteology of the head. It is clear, however, that the midsection of the body is faulted away, and that the tail clearly shows a greater num-ber of fin rays than endoskeletal supports.

Diplocercides kayseri Stensiö (1922), the only species of the genus, typifies the family Diplocer-cidae. The postrostral skull roof, cheek, braincase, shoulder girdle, body and fin outlines are known and well studied, whereas pelvic and median fin plates are unknown. Small paired frontonasals, with irregular median postrostrals, lie over the ethmoid region and long parietals over the orbits. The skull roof posterior to the intracranial joint is essentially as in *Coelacanthus granulatus* except that the oper-culum does not articulate directly with the tabular. The cheek consists of four bones, which lack tight joints, and the operculum is the sole bone of the opercular flap. The shoulder girdle, as preserved, consists of cleithrum and clavicle without an extra-cleithrum. There are more caudal fin rays than en-doskeletal supports. A basipterygoid process and a posteriorly projecting antotic process link the palate to the ethmosphenoid portion of the neurocranium (Bjerring, 1973), and the two portions of the neu-rocranium are solidly ossified.

A degree of confusion exists about the systematics and morphology of *Diplocercides* and *Nesides schmidti* (Stensiö, 1937). Stensiö states that he se-lected a specimen from among several *D. kayseri,* sectioned it, and subsequently decided that it was sufficiently different from unsectioned and less com-plete *D. kayseri* to warrant the erection of a new genus and species. There are certainly differences; some, like degree of endocranial ossification, can be accounted for by differences in growth stages, and some, like dentition, could be either preservational or of taxonomic significance. The relationship be-tween the two genera, however, remains to be ad-equately explored and the significance of the degree of endocranial ossification becomes dubious.

To summarize family-level taxonomy and sys-tematics of the coelacanths is relatively easy. There is no way to distinguish the Rhabdodermatidae from the Coelacanthidae on the basis of currently pub-lished information. Diplocercidae differ from Coel-acanthidae in having: a greater than one to one ratio of fin rays to endoskeletal supports; several median elements in the postrostral region; four, somewhat larger, but loose cheek plates; a small basipterygoid process; and possibly in having a greater degree of endocranial ossification in the adult stage.

One of the five Bear Gulch Limestone coel-acanths, *Caridosuctor populosum,* has a suite of characters enabling its assignment to a recognized family, the Rhabdodermatidae. The remaining three well-preserved species agree in the common pos-session of a character suite uniquely primitive among described coelacanths and as such, represent a dis-crete taxonomic unit. This taxonomic unit will be considered as a single family and suborder, in con-trast with the coordinate unit containing either more derived but presumed extinct Diplocercidae, the contemporaneous Rhabdodermatidae, or the prob-lematical species "*Coelacanthus*" *huxleyi.* The members of this new suborder share no obvious advanced characters, do not fall into any morpho-logical arrangement suggestive of subordinate taxo-nomic groupings, and are not comparable to any fish outside the Bear Gulch fauna. They do, how-ever, occupy a unique morphlogical and evolution-ary position among the Coelacanthiformes.

The following suite of characters is used as

guidelines for familial diagnoses: condition of the premaxilla and the rostral bones; presence or absence of the antorbital; number of series of bones of the supraorbital canal; presence and condition of supratemporal; number of bones and association in the cheek; presence or absence of a basipterygoid process; presence or absence of a suboperculum; condition and position of the pelvic, anal, and second dorsal fin plates; and the ratio of caudal fin rays to endoskeletal supports.

SYSTEMATIC PALEONTOLOGY

Order Coelacanthiformes
Suborder Coelacanthoidei

Type family.—Coelacanthidae Agassiz, 1839.

Diagnosis.—Nasal-frontal-parietal series of bones flanked laterally by a single supraorbital canal series of bones, the supraorbital canal lies lateral to the margins of the nasoparietals. A supratemporal bone either greatly reduced or absent. May be five or fewer, loosely associated bones in cheek. Opercular flap supported only by an opercular bone. Second dorsal fin articulates with posterodorsal margin of its basal plate. Anal fin plate located in ventral body wall anterior to firs haemal spines, and posterior to anus.

Included families.—Coelacanthidae (type), Rhabdodermatidae, Laugiidae, Diplocercidae.

Family Rhabdodermatidae Berg, 1958

Type genus.—Rhabdoderma Reis, 1888.

Diagnosis.—Paired premaxillae unornamented, ascending lamina of each perforated by a large pore for rostral organ. Bones of ethmoid commissure and rostral area small, unornamented, loosely in contact with each other and border large lateral line canal pores. Frontonasals paired, ornamented, and meeting in dorsal midline. Single series supraorbital canal bones lies lateral to frontonasals and parietals. Antorbital present, perforated by two rostral organ pores, and bordering posterior narial opening posterodorsally. Infraorbital canal bones as in Coelacanthidae, the postorbital set posterior to intracranial joint. Cheek bones five in number, thin, completely covering the cheek, with tight or overlapping sutures. Operculum the sole bone in opercular flap. Skull roof of the oticooccipital portion consists of a pair of long postparietals, flanked by reduced supratemporals anterior to posterolateral tabulars. Postparietals contain a lateral and a posterior pit line. Supratemporal contains anterior half of otic canal, which joins infraorbital canal from postorbital and passes into tabular posteriorly. Five extrascapulars present. Anocleithrum apparently not in contact with the braincase. Median and paired fin supports essentially as in Coelacanthidae except that pelvic plates are extended anterolaterally and anal fin support may not ossify. Caudal fin rays each have one endoskeletal support.

Genus *Rhabdoderma* Reis, 1888

Type species.—Coelacanthus elegans Newberry, 1856.

Diagnosis.—Premaxilla with few, large teeth, other tooth bearing bones of palate and lower jaw with fine granular teeth. Lateral borders of frontonasals and parietals indented to receive supraorbital canal bones, and each supraorbital pore bordered by parts of three bones. Tabular projects posteriorly beyond rear margin of postparietal. Preopercular canal in squamosal bears prominent pores dorsal to intersection of ascending and anterior canal branches. Shoulder girdle unornamented in smaller individuals. Anal fin support unossified. Ornamentation on skull roof (except tabular) antorbital and postrostral of fine tubercles, preoperculum of coarse tubercles, and remaining head bones of fine linear ridges.

Included species.—R. elegans Newberry, 1856; R. lepturus Huxley, 1866.

Remarks.—A morass of names have been proposed in the past, on the basis of isolated bones from the British Coal Measures (Moy-Thomas, 1935, 1937). There seems to be no way to define any of them with material presently available. *R. exiguum* (1908), while represented by several whole specimens (Schultze, 1972) has never been adequately described and is best omitted from any definite assignment at present.

Rhabdoderma elegans Newberry
(Figs. 2–12)

Synonymy.—R. ornatus Newberry, 1856. (R. robustus Newberry, 1856.)

Cotypes.—AMNH 503, 656.

Horizon and locality.—The cannel shale below the Upper Freeport coal, Allegheny Group, Late Westphalian D, from the Linton mine, Saline Township, Jefferson County, Ohio.

Diagnosis.—Moderate sized *Rhabdoderma,* up to 32 cm in length, with three paired frontonasals, two

Fig. 2.—*Rhabdoderma elegans,* CM 23025a. Scale = 1 cm.
Fig. 3.—*Rhabdoderma elegans,* CM 23025b. Scale = 1 cm.

anterolateral rostrals, four supraorbitals between postorbital and antorbital, and eight anterior supraorbitals. Terminal pore of supraorbital canal and transverse and posterior pit lines are prominent. Supratemporal narrow and bears several otic canal pores, tabular bears two to three large dorsomesially directed pores. Ethmoid region broad and shallow, postorbital, squamosal and quadratojugal are tall. Squamosal bears two large pores dorsal to anterior limb of the preopercular canal. Quadratojugal, angular and gular bear transverse pit lines. Operculum taller than wide. Skull ornamentation of tightly packed tubercles and ridges from the onset of ornamentation through adulthood. Palatal dentition of fine, slightly diverging lines of denticles, dorsally arched and fusing into thin ridges posteriorly. Body slender, pelvic plate extended anterolaterally by three processes. Anal plate unknown, and fin rays unornamented.

Description

Occurrence.—Rhabdoderma elegans is abundant at the Linton locality, but most specimens range in size from around 10 to 20 mm in gular length. Few are preserved with intact bodies and the small size of individual blocks of matrix results in the retrieval of very few complete fish. A complete specimen of 10.4 mm gular length (Figs. 2, 3), 49 mm in standard length, shows only the first few tuberculations developing on the postparietal and was evidently a very young individual. The largest known specimen (CM 23012) is a poorly preserved head with a gular length of 56.7 mm. Assuming linear growth relationships a standard length of 321.6 mm can be estimated for CM 23012. There are few elements of intermediate size between the two extremes. It is quite plausible that the Linton oxbow lake served as a spawning ground for *Rhabdoderma* females.
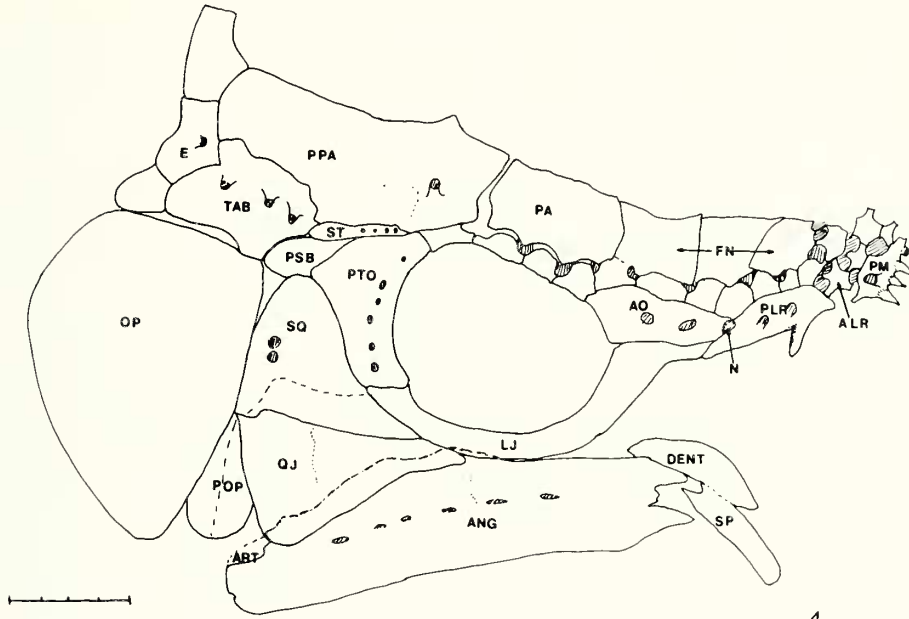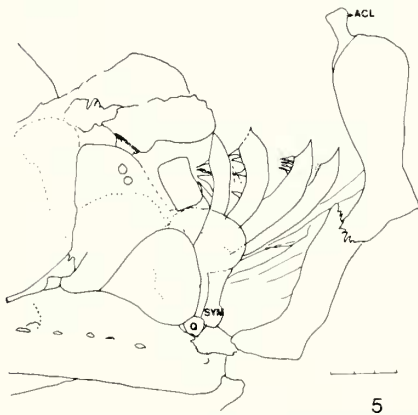
Fig. 4.—*Rhabdoderma elegans,* head restoration based on CM 23178, 23179, and 23180. Scale in mm. Abbreviations: ALR, anterolateral rostrals; ANG, angular; AO, antorbital; ART, articular; DENT, dentary; E, extrascapulars; FN, frontonasal series; LJ, lacrimojugal; N, naris; OP, operculum; PA, parietal; PLR, posterolateral rostral; PM, premaxilla; POP; preoperculum; PPA, postparietal; PSB, prespiracular; PTO, postorbital; SP, splenial; SQ, squamosal; ST, supratemporal; TAB, tabular.
Fig. 5.—*Rhabdoderma elegans,* CM 23179b, branchial region. Scale is in mm. Abbreviations: ACL, anocleithrum; Q, quadrate; SYM, symplectic. See Fig. 7.

The spacing of ornamentation on the skull bones is highly variable among small individuals of the same or similar sizes (Figs. 6–11). Growth of individuals evidently resulted in the addition of more tubercules with little increase in their size, although there seems to be a fair measure of individual variation in tubercle size itself. Bones of the largest individuals are densely tuberculated.

Ethmosphenoid.—The premaxilla (Figs. 6, 8) bears three or four teeth and usually shows one additional

tooth base, an indication of a possible replacement position. The premaxilla articulates by narrow facets with a small median rostral and two anterolateral rostrals. The dorsal border of the premaxilla is emarginated between the facets for large pores, and there is a deep notch between the posterior end of the premaxilla and the posterolateral rostral where the anterior narial opening of *Latimeria* is located (Millot and Anthony, 1958).

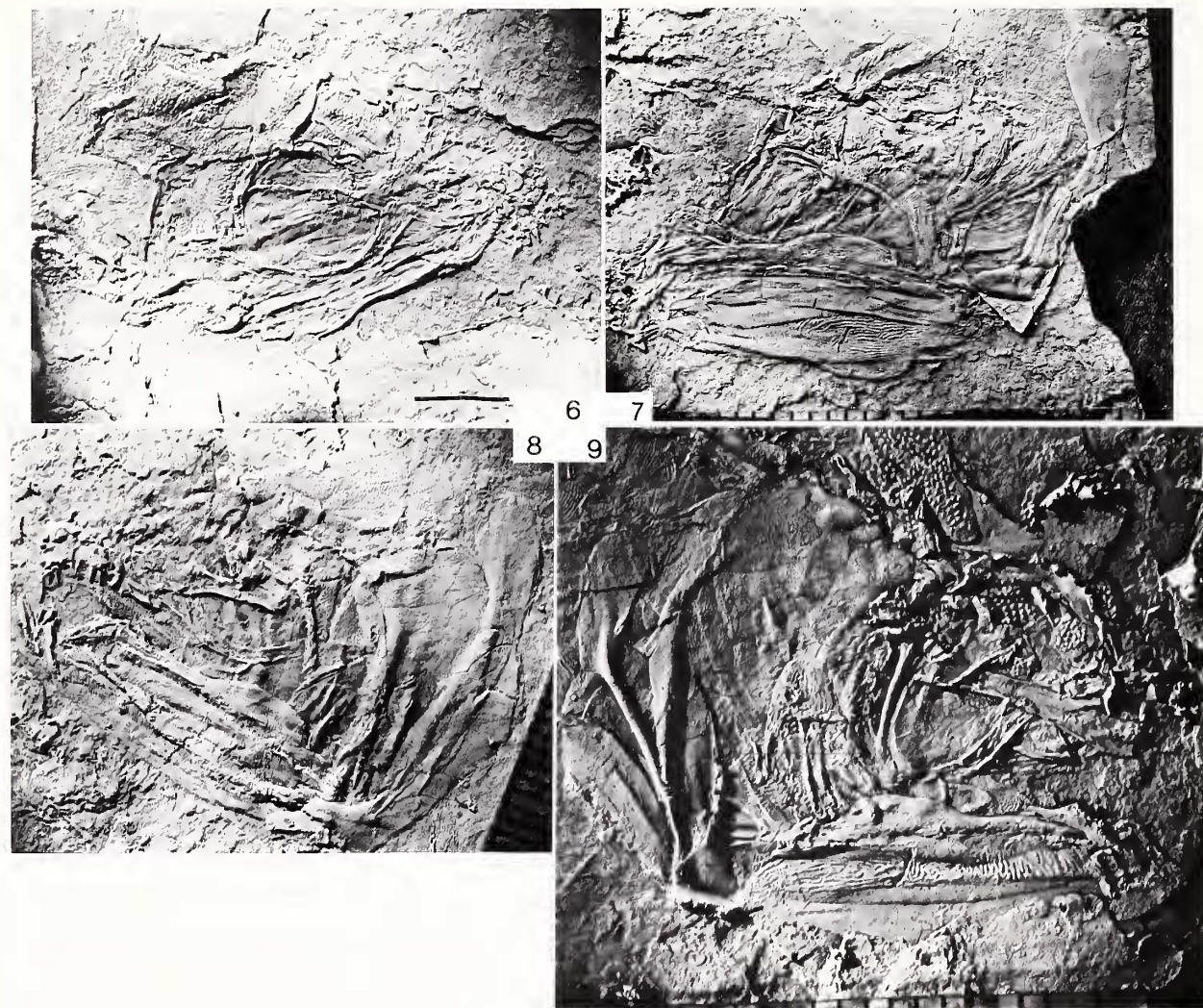The rostral is followed in the midline by a slightly

Fig. 6.—*Rhabdoderma elegans,* latex peel of head, CM 23179a. Scale is 5 mm.
Fig. 7.—*Rhabdoderma elegans,* latex peel of head, CM 23179b. Scale in mm.
Fig. 8.—*Rhabdoderma elegans,* latex peel of head, CM 26250. Scale in mm.
Fig. 9.—*Rhabdoderma elegans,* latex peel of head, MV 5564. Scale in mm.

larger, highly emarginated median postrostral. Posterior to the rostro-postrostral series are two other small, emarginate bones, the most anterior of the supraorbital canal bones. These bones are bordered posteriorly by the anterior edge of the frontonasal, and the more mesial of the two articulates by small facets to the adjoining elements. Three series of large pores, therefore, can be seen to traverse the snout between the frontonasals and the premaxillae, in addition to the premaxillary pore.

The three frontonasals are flanked laterally by eight anterior supraorbital elements (the tectals of Jarvik, 1942), and the supraorbital canal pores each occur between the edge of the frontonasal and two adjacent anterior supraorbitals. Lateral to the supraorbitals, bordering the two anterior frontonasals and posterior to the anterolateral rostrals is the large, thin posterolateral rostral. A conspicuous process projects ventrally from the anterior aspect of its ventral border (Fig. 4). This process forms the posterior border of the anterior nostril in *Latimeria* (Millot and Anthony, 1958), *Macropoma* (Watson, 1921) and can also be found in the Devonian *Onychodus* (Andrews, personal communication). Two large pores of the infraorbital lateral line canal perforate the posterolateral rostral, and its posterodorsal edge
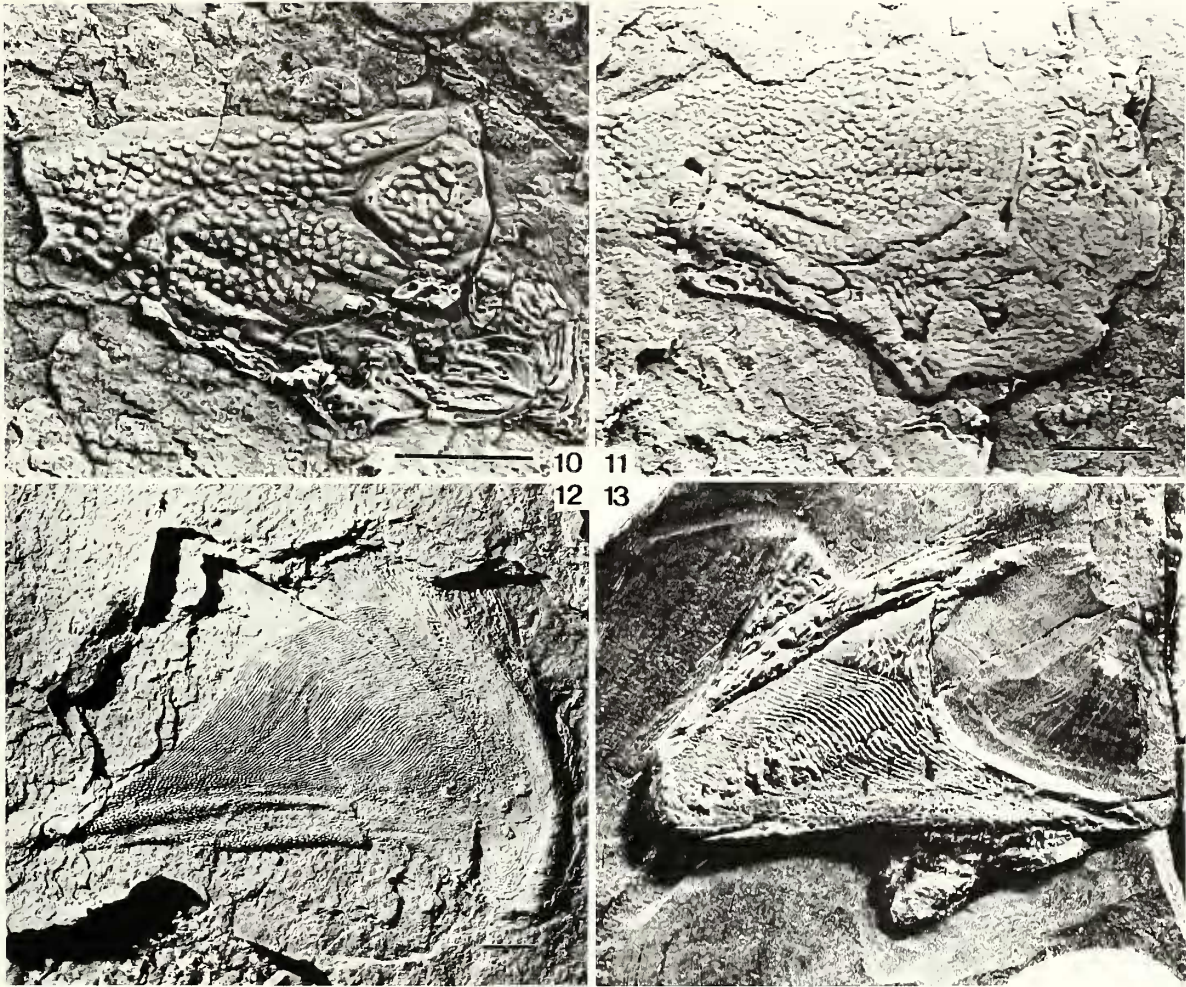
Fig. 10.—*Rhabdoderma elegans*, latex peel of left skull table with supernumary bone, CM 35246. Scale is 2 mm.
Fig. 11.—*Rhabdoderma elegans*, latex peel of left skull table with two supernumary bones, CM 25228. Scale is 2 mm.
Fig. 12.—*Rhabdoderma elegans*, latex peel of right endopterygoid, CM 23631b. Scale is 2 mm.
Fig. 13.—*Rhabdoderma lepturus*, latex peel of left endopterygoid, Hancock Museum 960-31.

is notched, in correspondence with a notch in the antorbital, in a position corresponding with the location of the posterior nostril of *Latimeria* (Millot and Anthony, 1958). The antorbital is long and low, perforated by two large pores corresponding in position to rostral organ pores of *Latimeria*. It is bordered ventrally by the anterior end of the lacrimojugal and anteroventrally by the posterolateral rostral. The most anterior of the three true supraorbital bones fit onto the posterodorsal corner of the antorbital. The short parietal covers the interorbital area, bearing an anteroventrally projecting ethmoid lamina. The antotic process projects posterolaterally from under the posterolateral corner of the parietal.

The posterior supraorbital lies lateral to the postparietal and antotic process, posterior to the intracranial joint.

The dermal bones of the ethmosphenoid region abut against each other loosely across the dorsal midline as well as elsewhere. There are no firm, tight contacts between any two bones in any individuals of any size. There is considerable variability in the relative sizes and shapes of the contralateral frontonasals as well as among individuals.

Cheek.—The postorbital, squamosal, lacrimojugal, and quadratojugal are well ossified, with overlapping or firmly butted junctions. The prespiracular is thin and fits directly against the curved

anteroventrolateral lamina of the tabular in a manner which leaves no doubt that it formed a spiracular operculum (Fig. 6). The preoperculum is a thin bone with relatively few, coarse tubercles (Fig. 9). The preoperculo-mandibular lateral line canal traverses the preoperculum and part of the squamosal vertically, ending in two large pores in the squamosal (Figs. 6, 8, 9). Below these pores a horizontal limb carries the main canal forward to join the infraorbital at the postorbital-lacrimojugal junction. A vertical pit line is found in the quadratojugal.

The infraorbital canal joins the otic canal at the anterior end of the supratemporal at the level of the lateral pit line of the postparietals (Figs. 4–6, 10, 11). There is no evidence in favor of a direct junction between supraorbital and otic canals. The supratemporal is loosely sutured to the postparietal. The contralateral postparietals abut loosely in small individuals but develop an anterior peg-and-socket suture with growth. At least four of 60 postparietals examined show evidence of an additional bone along the rear margin of the skull roof (Figs. 10, 11): this element tends to be obliterated by subsequent growth of bone and ornamentation. It is possible that it is this sort of supernumary bone that was found by Wenz (1975). A single specimen (Fig. 11) shows evidence of a duplicate supratemporal mesial to the canal bearer.

The dentary is thin, bears a few fine granular teeth, and forms the anterior edge of the broad lower jaw. A short vertical pitline rises from the mandibular canal directly under the coronoid bone. The splenial and the angular bear large mandibular canal pores. The coronoid (Figs. 6–9) is quadrangular and relatively long based, with a prominent dorsally oriented saddle and a noticeable anterior inclination. The coronoid bears circumferential rows of fine teeth on its oral surface, and fits mesial to the lacrimojugal immediately anterior to the quadratojugal. The coronoid of *Latimeria* supports extensive labial folds at the corner of the mouth. There is an extensive area of overlap between angular and gular (Figs. 7–9) ventral to the canal pores. The symplectic is long and prominent, and the single articular has both dorsally and mesially facing facets for the quadrate as well as a more posterior articulation for the symplectic. The retroarticular is separately ossified (Fig. 9) in smaller individuals.

The main features of the shoulder girdle are displayed in Figs. 7–9, but it should be noted that the anocleithrum is short, stubby, and does not seem to contact any element of the cranium. Only the largest cleithra (CM 23012) show ornamentation on

their posterodorsal corners. The gills are arranged as in *Latimeria* (Millot and Anthony, 1958) (Fig. 7), and bear clusters of sharp teeth.

Postcranium.—The axial skeletons of small specimens show 30 thoracic and 18 ossified caudal vertebral arches (Figs. 2, 3) although larger specimens may show up to four more posterior arches. The first nine or 10 neural arches are wide with very short neural spines and constitute a functional cervical region. The first dorsal fin plate (rarely visible and never clear) originates at the end of the cervical region, and the second dorsal support is intercalated between neural spines in the area around segments 26 and 27. The dorsal and ventral lobes of the caudal fin originate at around segment 35, with one or two free floating endoskeletal supports of the reduced leading rays. There are almost invariably one or two more rays in the dorsal (2–3+10–11) than in the ventral lobe (2–3+9–10) of the caudal fin. The rays of the fins are only distally segmented, and fin outlines are rounded.

The pelvic fins contain numerous rays. The pelvic plates were braced across the midline by a mesial process with an interdigitating suture, and anterolateral processes of the pelvic plate braced the pelvis in the body wall (Fig. 73). The anal plate is unknown. The second dorsal plate is very thin with no well developed articular area, but the axis of the fin evidently attached at the posterodorsal edge, as in modern coelacanths.

Discussion.—Forey (1981) has redescribed material from the British Carboniferous under the name of *Rhabdoderma elegans*. The principal diagnostic characters are the "kidney shaped" first dorsal fin plate, which cannot be demonstrated in the type material, and the convergent ornamentation of the scales, which is of dubious value. There are also several serious anatomical differences between *Rhabdoderma elegans* as defined on the basis of material from the type locality, and the British material that may preclude a relationship even at the generie level. The coronoid of *R. elegans* is quadrangular, although with a dorsal saddle and some forward inclination, whereas the coronoid of the British species is interpreted as triangular. The supraorbital canal connects to the otic canal in the tabular via a transverse supraorbital commissure traversing the edge of the postparietal in the British species, whereas in *R. elegans* there is no visible canal in the postparietal and there is a small free supratemporal between postorbital and tabular. The terminal pore of the supraorbital canal is prominent in *R. elegans* but not present in the British species.

Further, the transverse and posterior pit lines differ strongly between the two species. The tabular of *R. elegans* projects well beyond the rear margin of the postparietal and is perforated by few, large pores for the otic canal, features not seen in the British material. There are also differences in the squamosals, the numbers of vertebral arches and the proportions of the cleithrum, extracleithrum and clavicle. Finally, *Rhabdoderma elegans* apparently lacks an ossified anal plate. Although the snout of the British species is obviously very incompletely known, the premaxilla is very similar to that of other known Rhabdodermatidae in bearing a perforation for the rostral organ. Contrary to Forey's assertion, however, there is no evidence that the ethmoid commissure was carried by the premaxilla (see below). The British species cannot reasonably be assigned to the genus *Rhabdoderma*, and certainly cannot be considered conspecific with *R. elegans*.

Comments on Rhabdoderma lepturus

A few specimens of whole and partial heads of *R. lepturus* (Huxley, 1866) from Newsham Colliery, Northumberland, were available for study. The quality of preservation of these specimens did not permit detailed comparison with *R. elegans*, and the specimens were preponderantly from moderate and large-sized individuals. *R. lepturus* differs from *R. elegans* in a number of small details, such as: having a tabular which projects less prominently both laterally and posteriorly; a posterior pit line continuous nearly to the posterior margin of the skull; and in having increasingly sparse ornamentation on the parietals, postparietals and gulars with increasing size. The gulars also lack a prominently tuberculated mesial zone and have a greater area ornamented by transverse ridges. The palates differ in proportions (Figs. 12, 13). The pelvic girdle of *R. lepturus* differs in having a long, angular articular process and the second dorsal fin plate resembles the coelacanthid condition. There are no obvious differences in premaxillae, lower jaws or shoulder girdles. It would be difficult at present to distinguish small individuals of the two species without better specimens.

Comments on Coelacanthus huxleyi

Traquair (1881) described a new species of coelacanth from the Visean of the Esk Valley of Dumfriesshire, Scotland, on the basis of a number of small individuals. The largest individual is only 76 mm in standard length and preservation of the skulls is poor. Sufficient cranial and postcranial information is available however (even in Moy-Thomas,

1937) to recognize that the unique morphology of "*C.*" *huxleyi* necessitates its assignment to a new genus outside the scope of coelacanth families as presently understood.

Incertae Familiae

Genus *Dumfregia*, new genus

Type species.—*Coelacanthus huxleyi* Traquair, 1881.

Diagnosis.—Small coelacanths with skull roof firmly sutured across the midline and longitudinally furrowed. Antorbital present, suboperculum lacking, and palate suspended directly below intracranial joint, indicating a very short antotic process. Dermal ornamentation appears confined to few coarse longitudinal lines on the gular; operculum and skull roofing bones smoothly finished. Six cervical, 19 trunk and up to 22 caudal neural arches. Ossified ribs present in trunk. First dorsal fin originates over eighth neural arch and stem of second dorsal fin intercalated above 23rd neural arch. Basal plate of second dorsal fin is rounded and fin axis originates directly above basal plate. Pelvic plate long and composed of a trough-like element appearing to be lamellar bone anterior to a short, cancellous looking region with short narrow processes facing posteriorly and laterally; the two plates broadly joined in the midline. Anal plate with ventral lamina and a posterodorsal process braced against first complete haemal spine. There are 3–4+11–13 dorsal caudal rays, +12–14 ventral caudal rays, and an equal number of endoskeletal supports.

Etymology.—*Dumfregia*, latinization of Dumfries, the shire in which the specimens were found.

Dumfregia huxleyi (Traquair)
Figs. 14, 15

Synonymy.—
Coelacanthus huxleyi Traquair, 1881.
Rhabdoderma huxleyi Reis, 1888.
Coelacanthus huxleyi Woodward, 1891.
Coelacanthus huxleyi Aldinger, 1931.
Rhabdoderma huxleyi Moy-Thomas, 1937.
Rhabdoderma huxleyi Forey, 1981.

Type specimen.—IGS-GSE 4693.

Referred specimens.—IGS-GSE M2149, 2297c, 5644, 5645. RSM 1885-54-6, 1885-54-7, 1885-54-9, 1891-53-4, 1978-43-1.

Horizon and locality.—Visean C_2S_1 Lower Carboniferous Glencartholm volcanic beds, Upper Border Group in the river Esk, Dumfriesshire, Scotland.

Diagnosis.—As for genus, the only known species.

Discussion.—Unlike the Rhabdodermatidae, the

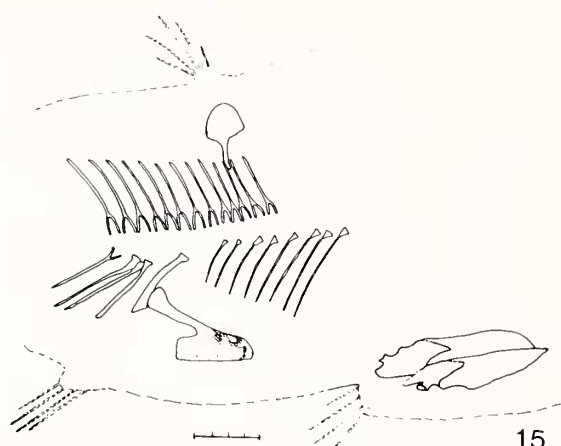Fig. 14.—*Dumfregia huxleyi*, midbody, RSM 1885-54-9. Scale in mm.

Fig. 15.—*Dumfregia huxleyi*, midbody, RSM 1885-54-9. Scale in mm.

head of *D. huxleyi* shows no evidence of ornamentation and is not roofed with loosely abutted, flat bones. It is, instead, constructed of two highly sutured units longitudinally grooved to maximize resistance to bending deformation. The architecture of the head, as known, resembles that of coelacanthids although an antorbital seems to be present. It is interesting, if of unknown significance, that prominent otoliths are preserved in virtually every skull. An ossified swim bladder is occasionally in evidence.

The second dorsal fin plate (Figs. 14, 15) is a rounded, thin plate upon a thin intercalary stem, and unlike either rhabdodermatid or coelacanthid conditions the fin axis does not arise from the posterodorsal limb of a T-shaped plate, but directly above the rounded plate. The primitiveness of this character will be discussed later in this paper.

The pelvic plates are evidently compound structures in origin with an anterior troughlike lamellar-bone plate and a posterior unit. They are far simpler in morphology than rhabdodermatid plates in lacking any anterolateral or medial processes. While coelacanthid pelvic plates also bear a medial process (Fig. 73), they, like *Rhabdoderma,* show a cancellous zone only at the articulation of the axis of the fin. Only *Undina minuta,* as illustrated by Schaeffer (1941), has a similar pelvic plate, although Stensiö (1921) indicates that the pelvic plates of *Laugia* might be compound as well as complex.

All previously described coelacanth anal plates have been unsupported in the ventral body wall anterior to the first haemal spines. The bracing of the anal plate against the haemal front is an approach to the primitive condition of endoskeletal support as seen in several Bear Gulch coelacanths, in Rhipidistia (Andrews, 1973), and in Actinopterygii (Lowney, 1980). There is a unique mixture of advanced and relatively primitive characters in *Dumfregia* that makes it difficult to place in the context of coelacanth systematics at present.

The Glencartholm volcanic beds are generally considered to be marine on the basis of their invertebrate fauna (Lumsden et al., 1967). It must be noted that collection was accomplished with the aid of blasting powder which tended to obscure precise stratigraphic relationships. The presence of apparently fresh water ostracods among the coelacanths reinforces the observation that the marine invertebrates and many of the fish do not occur in the same layers (R. B. Wilson, personal communication). It is plausible to postulate an estuarine or other mixed environment for *Dumfregia huxleyi.*

BEAR GULCH COELACANTHS

Family Rhabdodermatidae

Genus *Caridosuctor* Lund and Lund, 1984

Type species.—*Caridosuctor populosum* Lund and Lund, 1984.

Diagnosis.—Marine rhabdodermatids that differ from other genera in having large teeth on dentary, precoronoids, and ectopterygoid. Preorbital region higher and more rounded than in other members of the family, cheek bones deeply overlap each other and operculum, operculum articulates with tabular and posterior margin of the tabular level with posterior margin of skull. Ornamentation of tubercles
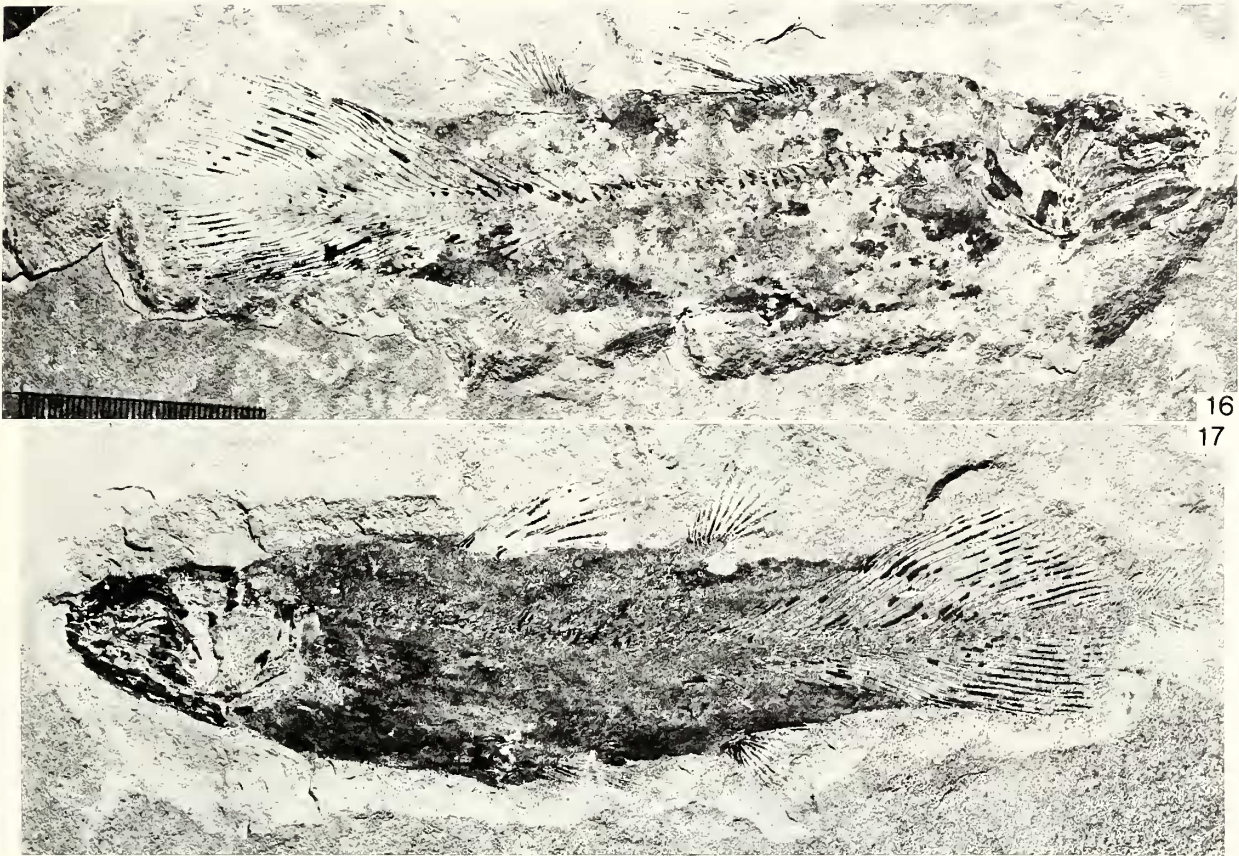
Fig. 16.—*Caridosuctor populosum,* Type, MV 6021a. Scale in mm.
Fig. 17.—*Caridosuctor populosum,* Type, counterpart, MV 6021b.

sparse on skull roof and preorbital region, dense in large specimens on very thin cheek bones, and of dense vermiform ridges on operculum and angular of lower jaw posterior to angular pit line. First dorsal fin plate has ventral digitiform processes, second dorsal plate anteroposteriorly elongated and bears an articulation for the fin posteriorly, and anal plate, which rarely ossifies, a simple rod in ventral body wall anterior to first haemals. Pelvic plates very broad anteriorly, with three major and one minor anterior lateral processes.

Caridosuctor populosum Lund and Lund, 1984
Figs. 16–34

Previous reference.—"Long body," Lund et al., in press, Fig. 1.

Type specimen.—MV 6021.

Referred specimens.—MV 2557, 2804, 2917, 2924, 2928, 2997, 3092, 3567, 3570–3572, 3576, 3626, 3632, 3633, 3759–3761, 3820, 3861, 5547, 5548, 6022–6040, 6208–6214, 6939–6944, 7702. CM 25590, 27299–27306, 27309 (counterpart, 27311), 27310, 27312 (counterpart, 27313), 27314–27332, 30671–30710, 30717–30723, 35203, 35528–35536, 35675–35678, 37513–37519, 41067.

Horizon and locality.—Namurian A (E2B), Lower Carboniferous Bear Gulch Limestone member of the Heath Formation, Big Snowy Group, south of Becket, Fergus County, Montana.

Diagnosis.—Coelacanth ranging from 30 mm to 217 mm in standard length, and of cylindrical body form. Caudal fin outline elliptical. Meristic characters are: Vert. segments, 9–11 cerv., 23–26 abd., 20–25 caud.; P^1, 13–15; P^2, 3–4+10–13; D^1, 3–4+7–9; D^2, 4–5+10–14; A, 2–3+10–13; caudal, dorsal rays, 3–4+14–16; caudal, ventral rays, 3–4+11–13. Proportional characters are given in Table 1.

Description.—The head length-standard length ratio describes a curve where the slope decreases markedly above about 120 mm in standard length, with very tight correlation (Fig. 20). Among meristic characters, variation in the number of precaudal segments is primarily related to coverage of the cer-

Table 1.—*Proportional statistics of* Caridosuctor populosum. *Abbreviations: Asp. R., aspect ratio of the caudal fin; GL/HL, gape length : head length; GL/LJL, Gape length : lower jaw length; GL/SL, Gape length : standard length; HL/SL, Head length : standard length; LJL/SL, lower jaw length : standard length; Max. ht./SL, Maximum body height : standard length; SD, standard deviation; Var., variance.*

Statistics	$\dfrac{\text{Max. ht.}}{\text{SL}}$	$\dfrac{\text{HL}}{\text{SL}}$	$\dfrac{\text{GL}}{\text{HL}}$	$\dfrac{\text{GL}}{\text{SL}}$	$\dfrac{\text{LJL}}{\text{SL}}$	$\dfrac{\text{GL}}{\text{LJL}}$	Asp. R.
Individuals over 100 mm							
N	15	13	13	14	14	14	12
Mean	.2256	.1596	.4894	.0784	.1565	.4936	.7989
SD	.0162	.0137	.0559	.0044	.0117	.0371	.0434
Var.	.0002	.0001	.0029	.00001	.0001	.0013	.0017
All pooled individuals							
N			16	17	16	17	
Mean			.4833	.0796	.1584	.4891	
SD			.0539	.006	.0135	.0352	
Var.			.0027	.00003	.00017	.00117	

vical series by the operculum and shoulder girdle, and becomes more marked with increasing size of the specimens. Variation in the number of caudal segments correlates directly with increasing size and consequent ossification of terminal elements. The taxonomic value of the meristic characters is limited, and will be discussed later in the paper. The taxonomic value of the proportional characteristics is very high in all Bear Gulch coelacanths.

The smallest known specimen, MV7702, is 30

Fig. 18.—*Caridosuctor populosum,* latex peel of head, CM 30723. Scale is 5 mm.
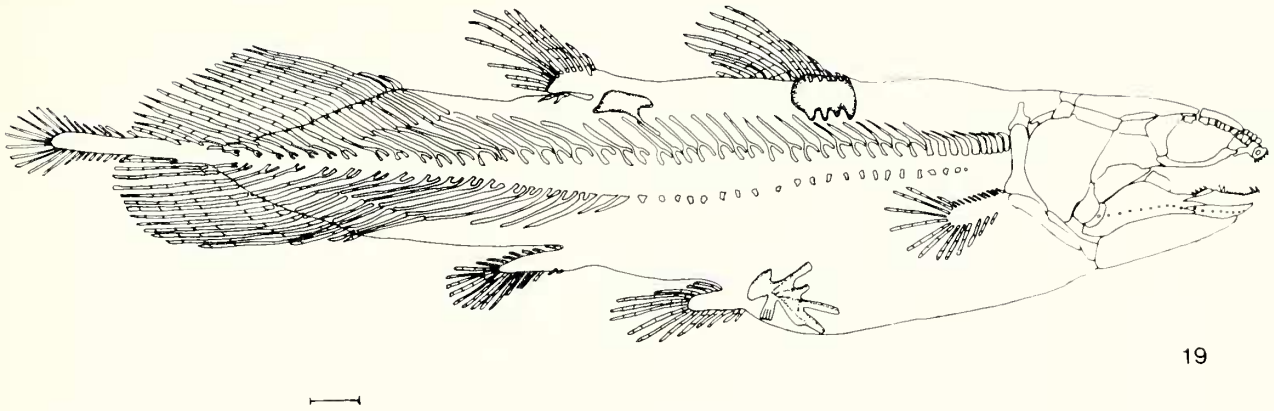
Fig. 19.—*Caridosuctor populosum,* restoration, based on CM 25590, MV 6021. Scale is 1 cm.

mm in standard length and lacks scales. One other, very small individual is known, CM 41067, with scales, standard length of 42 mm. These two specimens have not been included in the statistics. There is one 55 mm individual, CM 30703. Specimens of 79 mm standard length and above are abundant. The size distribution of specimens strongly suggests that *C. populosum* may not have spawned in the sampled part of the Bear Gulch basin.

Ethmosphenoid region.—The premaxilla (Figs. 18, 21), as in *Rhabdoderma,* bears three to five large

teeth, frequently with one of the tooth positions vacant. A large rostral pore perforates the ascending lamina. A small rostral bridges the gap between opposite premaxilla, followed by the anterior supraorbitals, then by a single postrostral. A single anterolateral rostral lies dorsal to the premaxilla and a large posterolateral rostral follows the premaxilla on the oral border. The contact between these two elements is minimal; at the posterior tip of the premaxilla, the anterior narial opening is located between them. The posterolateral rostral bears two or
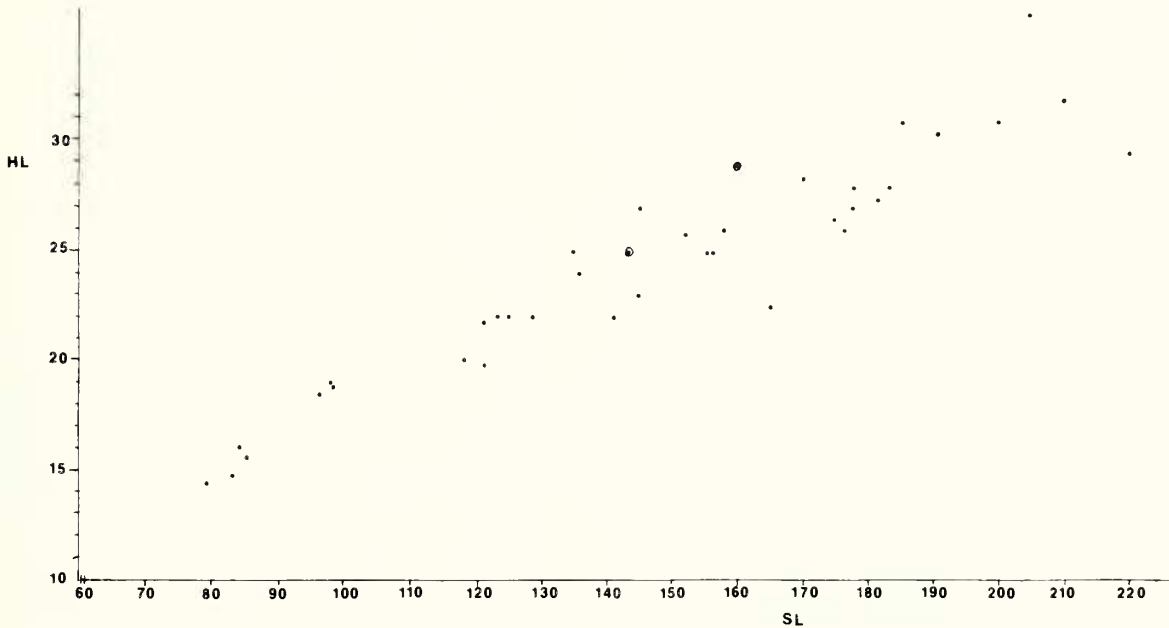
Fig. 20.—*Caridosuctor populosum,* graph of head length to standard length. Circled points = 2 specimens.
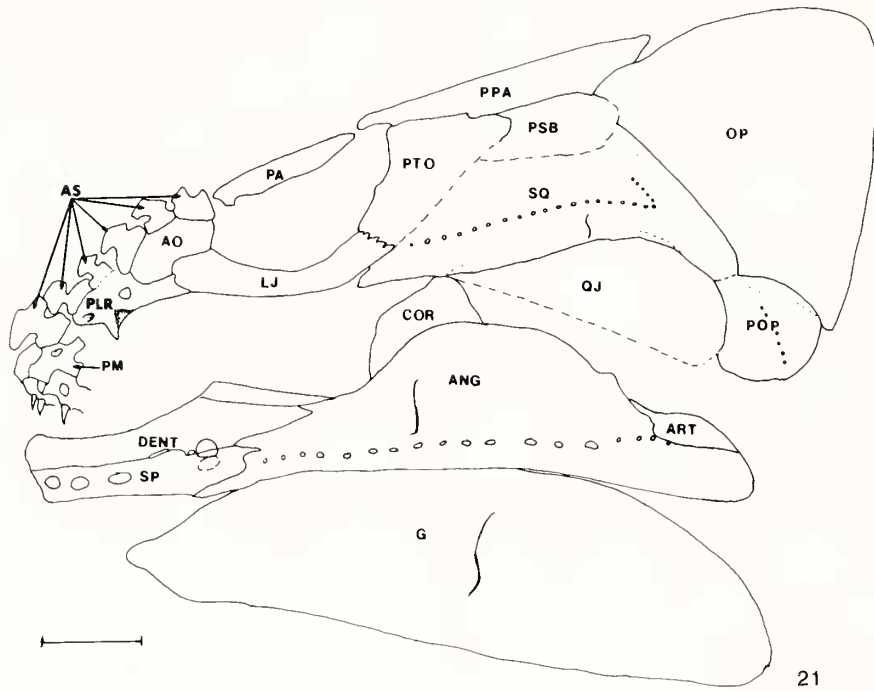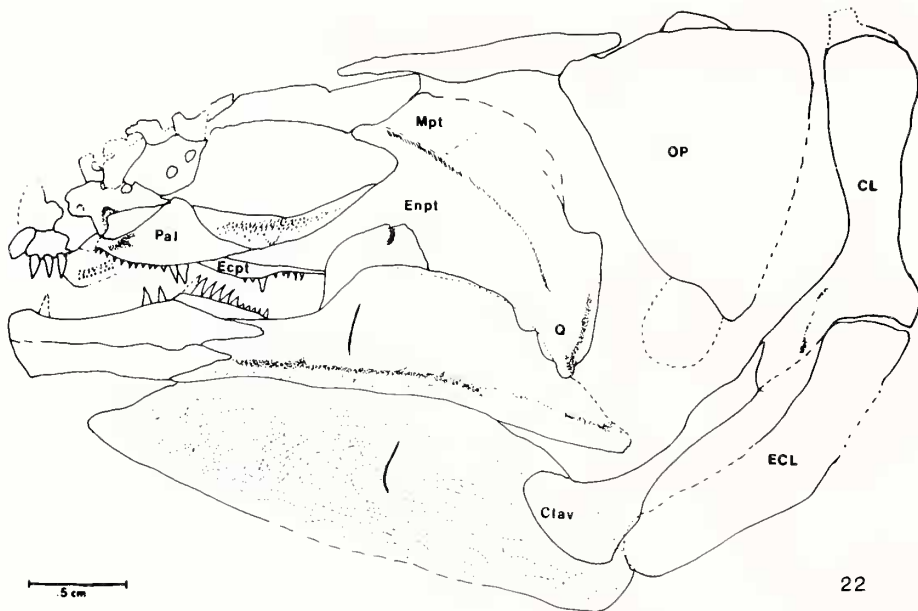
Fig. 21.—*Caridosuctor populosum,* dermal bones of the lateral surface of the head. From CM 25590. Scale is 1 cm. Abbreviations: AS, anterior supraorbitals; COR, coronoid; G, gular. Other abbreviations as in Fig. 4.

Fig. 22.—*Caridosuctor populosum,* deep view of left side of the head, based on CM25590. Scale is .5 cm. Abbreviations: CL, cleithrum; Clav, clavicle; ECL, extracleithrum; Ecpt, ectopterygoid; Enpt, endopterygoid; Mpt, metapterygoid; OP, operculum; Pal, autopalatine.

three infraorbital canal pores and a strong descending narial process, and probably forms the anterior border of the posterior nostril; a narrow posterior limb underlies the antorbital and contacts the lac-rimojugal posteriorly (Fig. 21). The antorbital bears two large pores which are considered rostral organ pores.

There are seven anterior supraorbitals and seven

Fig. 23.—*Caridosuctor populosum,* skull roof of the ethmosphenoid moiety, CM 30681. Scale is 2 mm.
Fig. 24.—*Caridosuctor populosum,* restoration of the skull in dorsal view, based upon CM 30681.
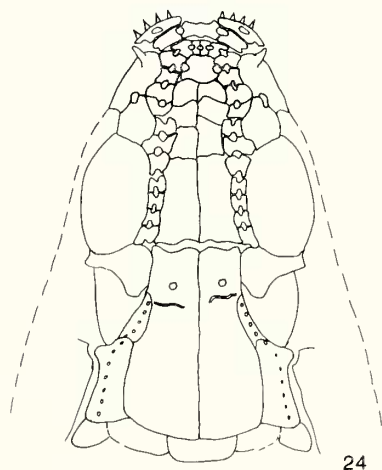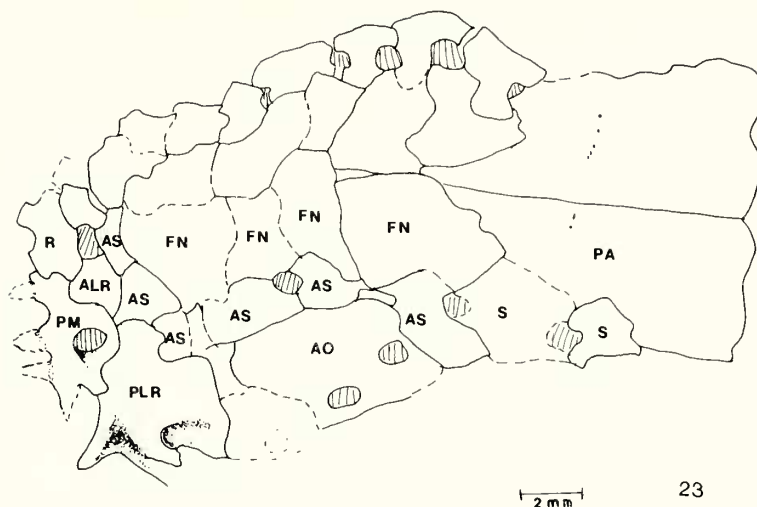
supraorbitals over the orbit, the most posterior of which lacks a pore and lies behind the intracranial joint. The supraorbital canal pores are bordered principally by canal bones (Fig. 23), and not significantly by the frontonasal bones as in *R. elegans.* The degree of bone emargination by pores in the rostral region is minimal although the rostral, post-rostral and premaxilla are emarginated and the precise shape of the anterolateral rostral cannot be determined. Of the above mentioned bones, only the more rearward of the anterior supraorbitals and the antorbital are ornamented with tubercles (Fig. 18).

There are generally four paired frontonasals anterior to the parietals, but asymmetry in numbers, size and shape of individual elements is common

(Figs. 18, 23). The frontonasals are all thin elements, each of which tends to develop an area of central tuberculation relatively late in ontogeny. The parietals roof the orbital region, form the anterior edge of the intracranial joint, and are laterally scalloped for reception of the mesial edges of five supraorbitals. They bear a slight ethmoid lamina anteroventrally. The frontonasals appear to occasionally fuse with each other, and the parietals maintain a tight sutural contact across the midline except in the smallest individuals, in contrast to the loose connections in all *R. elegans.* The overall condition of the dermal bones of the preorbital region can best be described as loose, thin and flexibly joined.

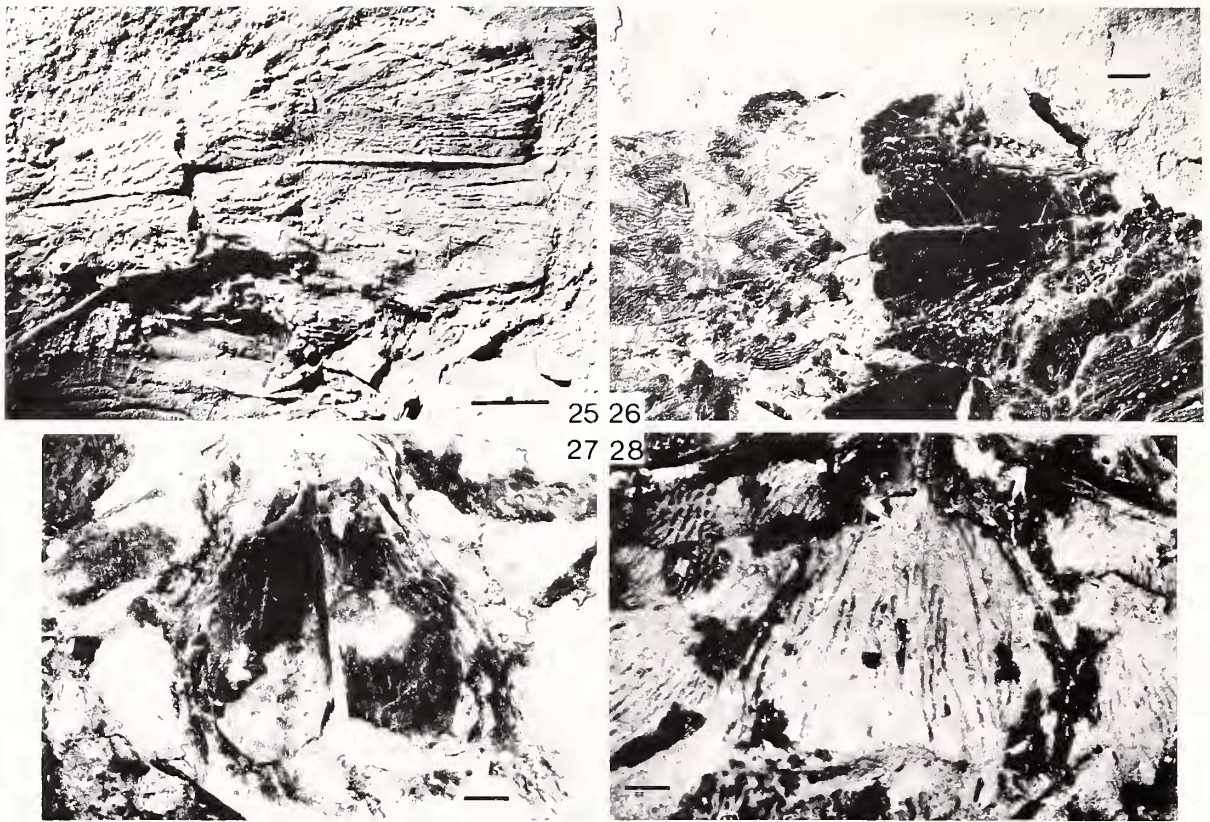*Cheek.*—The lacrimojugal is a thin, arcuate ele-

Fig. 25.—*Caridosuctor populosum,* latex peel of the skull roof from the parietals to the rear margin, CM 30681. Scale is 2 mm.
Fig. 26.—*Caridosuctor populosum,* skull table of CM 27299b. Scale is 2 mm.
Fig. 27.—*Caridosuctor populosum,* skull table of CM 27305a, photographed under alcohol. Scale is 2 mm.
Fig. 28.—*Caridosuctor populosum,* skull table of CM 27305b (counterpart of Fig. 27), photographed under alcohol. Scale is 2 mm.

ment that is sutured with the antorbital and posterolateral rostral anteriorly and the postorbital posteriorly at the quadratojugal-squamosal junction. Pores are rarely evident in the lacrimojugal except at its anterior end. The postorbital is longer than high, its posterodorsal extension tapering to a point and overlapping the long, thin prespiracular. The anterodorsal corner of the postorbital adjoins the postparietal well behind the intracranial joint at the level of the posterior end of the posterolaterally projecting antotic process (Figs. 23, 24). The infraorbital canal, after receiving the horizontal (jugal) limb of the preopercular canal at the lacrimojugal-squamosal junction, traverses the postorbital to join the otic canal at the anterior end of the supratemporal, midway along the dorsal margin of the postorbital.

The quadratojugal, squamosal and preoperculum are thin bones with relatively closely set tubercular ornamentation (Fig. 18). The quadratojugal extends from the posterior edge of the coronoid process to the posterior edge of the quadrate. The preoperculum is overlapped by the quadratojugal anteriorly and overlaps the anterior edge of the operculum posteriorly. Both quadratojugal and preoperculum are overlapped by the squamosal, which also overlaps the operculum. A long, thin oval prespiracular extends from under the rear of the postorbital to fit against the tabular. The cheek bones are heavily ornamented but virtually lack a basal lamellar layer, resulting in preservation so poor that the paths of lateral line canals or pit lines can rarely be located. The preopercular canal emerges vertically into the squamosal and thereafter extends anteriorly, to the infraorbital canal. No large pores are present in the squamosal. The quadratojugal pit line extends vertically into the squamosal as a prominent groove. The operculum is the sole bone of the opercular flap. The anterodorsal corner of the operculum bears a
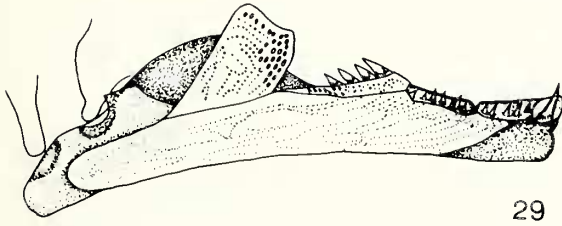
Fig. 29.—*Caridosuctor populosum,* restoration of internal view of the lower jaw, from CM 30723, 35530, MV 3567, 3761.
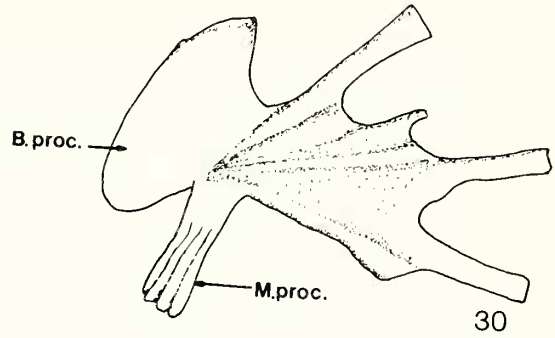

Fig. 30.—*Caridosuctor populosum,* pelvic girdle of CM 35203b. See Fig. 33.

well developed condyle and facet for articulation with the tabular (Fig. 18); the operculum projects considerably beyond the rear margin of the skull.

Oticooccipital.—The postparietal, the principal skull roofing bone of the oticooccipital part of the brain case, is bordered laterally by the narrow supratemporal and laterally expanded tabular (Figs. 24–28). The supraorbital canal cannot be seen to enter the postparietal, but can be seen to join the infraorbital canal above the postorbital (Figs. 25, 27). A pore and a faint lateral pit line are evident in the postparietal mesial to the anterior end of the supratemporal. The otic canal of the supratemporal continues into the tabular, opening to the surface by three large pores, and passes into the lateral extrascapular. There are five thin, scale-like bones in the extrascapular canal series, which carry the occipital commissure near their anterior edges.

The otic canal in *Latimeria* receives only the infraorbital canal, and passes into the tabular in soft tissue lateral to the postparietal in precisely the position of the reduced supratemporal of the Rhabdodermatidae. The significance of the lateral line canal paths of coelacanths will be discussed later in this paper.

Palate, lower jaw, and branchials.—The shapes, proportions and relationships of the bones of the palate and lower jaw are very similar to those of other coelacanths.

The triangular autopalatine is fringed with dermopalatine plates anteriorly and laterally, followed posteriorly by a long, thin ectopterygoid that extends to the level of the middle of the coronoid (Fig. 22). The dermopalatines and ectopterygoid bear prominent, finely striated teeth, whereas the endopterygoid bears posterodorsally oriented fine denticulated

ridges. The metapterygoid is only loosely attached to the endopterygoid and does not bear teeth orally; however, a mosaic of tooth bearing plates lies mesial to the metapterygoid in the roof of the mouth and extends anteriorly to the middle of the orbit. The palate is very strongly curved outward near its posterior border.

The dentary and the underlying splenial, which carries the symphysial end of the mandibular lateral line canal, are relatively short, thin bones. The dentary bears only two or three large teeth near its posterior end. There is a long dorsal concavity or diastema in the dorsal margin of the angular anterior to the coronoid eminence (Fig. 18). The angular slopes gently posteroventrally from the coronoid to the lateral edge of the articular facet, exends horizontally briefly and then slopes strongly to the posteroventral corner of the lower jaw. The angular does not cover the retroarticular region of the articular laterally. The mandibular canal exits in the splenial and anterior angular through large pores, decreasing somewhat in size posterior to the vertical pit line. The mandibular canal pores curve dorsally at the articular. The lower jaw bears no ornamentation anterior to the angular.

There is a series of tooth bearing plates mesial to the oral border of the dentary; the parasymphysial plate bears one large tooth and many finer ones, whereas the more posterior plates bear a few moderate sized teeth grading into fine teeth. The precoronoid slopes posteroventrally to the base of the coronoid, and bears several large teeth along its dorsal rim as well as very fine teeth on its mesial surface (Figs. 22, 29). The quadrangular coronoid has a prominent saddle-shaped dorsal edge, articulates with the dorsal edge of the prearticular ventrally,
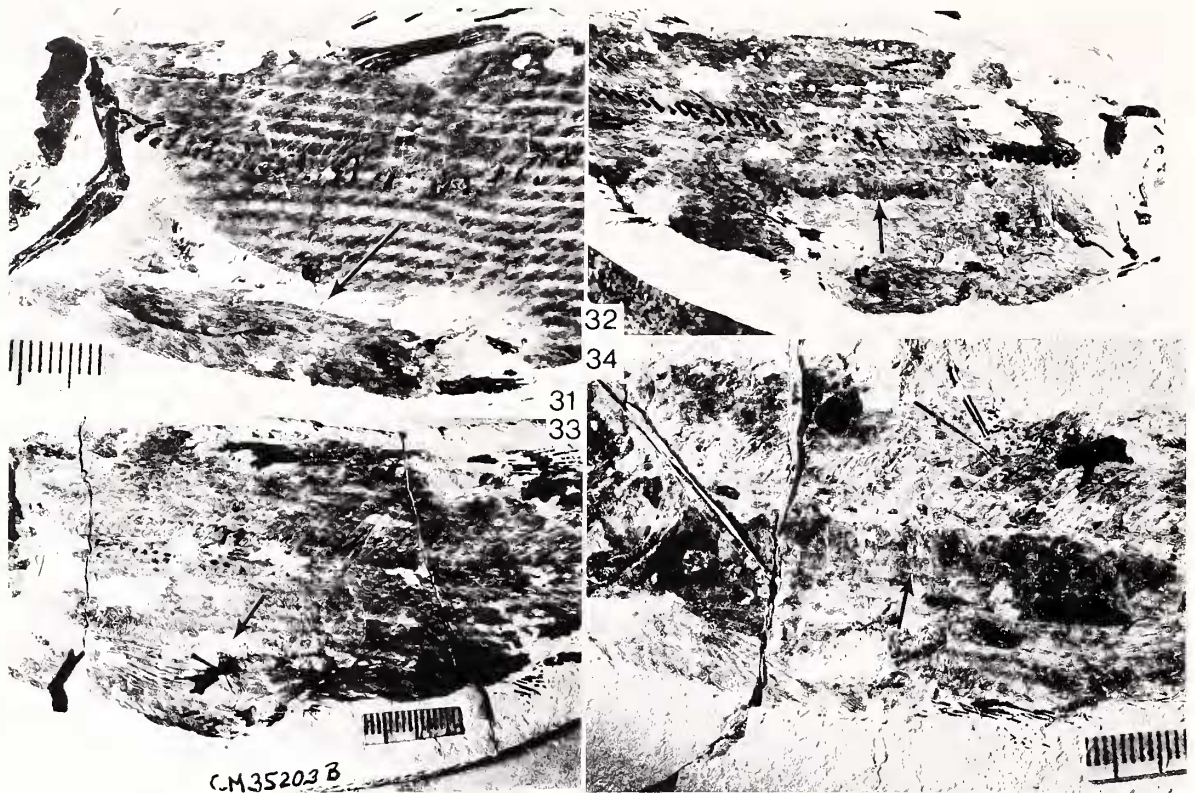
Fig. 31.—*Caridosuctor populosum,* CM 35675, midbody, scale in mm. Arrow points to intestinal filling.
Fig. 32.—*Caridosuctor populosum,* CM 35203a, same scale as Fig. 33. Arrow points to swim bladder.
Fig. 33.—*Caridosuctor populosum,* CM 35203b, scale in mm. Arrow points to fecal bolus.
Fig. 34.—*Caridosuctor populosum,* CM 35535, scale in mm. Arrow points to swim bladder.

and bears circumferential rows of rather blunt teeth anteriorly (Fig. 18) which become finer posteriorly and ventrally. In larger individuals the articular ossification is massive and includes the retroarticular region. In smaller individuals there is some reason to believe that there is a separate articular ossification for the quadrate condylar fossa anteriorly and ventrally, and a retroarticular ossification from the symplectic to the posterior corner of the jaw. The articular is most massive along the anterior wall of the fossa, and less massively ossified directly ventral to the quadrate.

Shoulder girdle.—The anocleithrum is a short element capping the cleithrum (Figs. 22, 31). There appears to be no direct bony contact with the braincase, again as in *Latimeria* (Millot and Anthony, 1958). The anocleithrum is rarely seen intact, however, and only the base is usually preserved. The cleithrum, clavicle and the extracleithrum show considerable ornamentation, but only in larger spec-imens. The clavicles meet in the ventral midline in a broad but very loose contact. The pectoral fin is borne at midflank, but while axial elements and the scapulocoracoid preserve as weak impressions they are never ossified.

Postcranial skeleton.—The first 9 to 11 neural arches are short, wide, and bear short spines inclined at a very low angle to the axis (Fig. 32). The angle of the succeeding three spines increases and the arches increase in height as they decrease in width (Fig. 19). The six neural spines underlying the first dorsal fin plate are of equal length, whereas those following the dorsal fin plate are noticeably longer except for the short neural spine bearing the second dorsal fin plate. The neural spines of the caudal region are longer than those of the thorax, each except the first three to four tightly associated with an epineural supporting a caudal fin ray. In most specimens the first epineural is free from attachment to a neural spine. Neural arches are borne upon all

caudal neural spines. The arches approach a horizontal attitude posteriorly, whereas the spines and epineurals show increasing anterodorsally concave arching. Fin rays in turn are angled posteriorly from their bases of attachment to the epineurals, and are only articulated over their distal halves.

Strong rib bases are present on all thoracic vertebral segments, but there are no indications of ribs. Two incomplete haemals form the transition to the long posteriorly sweeping and anteroventrally concave haemal spines. The haemal arches and spines approach a horizontal attitude toward the posterior end of the column, the infrahaemals being straight elements descending from them at a pronounced angle.

The fin rays in the caudal lobe are unsupported by endoskeletal elements.

Peritoneal cavity.—An extensive, but thinly ossified and either coiled or partially partitioned (Figs. 32, 34) swim bladder occupies the dorsal portion of the gut cavity. The digestive tract itself is not infrequently preserved with phosphatic infilling or ingested food, and extends without evident curvature from the pharynx to immediately between the bases of the pelvic fins (Figs. 31–34). Traces of chitin and occasional scales can be seen in the intestinal filling of several specimens. Coprolitic masses occasionally can be found directly above the pelvic girdle; these never show spiral twists nor identifiable particulate matter on gross examination. A spiral valved intestine, however, is indicated by the impressions left by partially filled intestines, and by the straightness and extensibility of the digestive tract. The entire longitudinal extent of the peritoneal cavity of CM 27318, 150 mm in standard length, is occupied by an intact paleostomatopod shrimp *Tyrannophontes theridion* (Schram and Horner, 1978) 50 mm in length that lies head posteriorly. This is regarded as evidence that the intestine can be extended posteriorly from above the anus to the posterior wall of the peritoneal cavity, to accommodate large prey items.

Suborder Hadronectoroidei Lund and Lund 1984

Type family.—Hadronectoridae Lund and Lund, 1984.

Diagnosis.—Nasal-frontal-parietal series anamestic in early ontogeny flanked by mesial and lateral supraorbital canal series, and mesial canal series tends to fuse with nasal-frontal-parietal series during ontogeny. Supratemporal bone unreduced. Cheek of five bones, tightly fitted or overlapping.

Opercular flap contains both opercular and subopercular bones. Postcranially, second dorsal fin axis articulates directly above its basal plate, anal fin plate directly below, and supported by, first haemal spines, and there is no extension of the peritoneal cavity posterior to the anus.

Included families.—Hadronectoridae, the only family presently known.

Family Hadronectoridae Lund and Lund, 1984

Type genus.—*Hadronector* Lund and Lund, 1984.

Diagnosis.—The same as for the suborder, only family.

Genus *Hadronector* Lund and Lund, 1984

Type species.—*Hadronector donbairdi* Lund and Lund, 1984.

Diagnosis.—Premaxilla bears a narrow dorsal lamina emarginated for one or more pores. Rostropostrostral series large, containing 6 bones and extending posteriorly to level of orbit. Lateral supraorbital bones fuse into 3 to 4 elements, mesial supraorbital bones very narrow over orbit. Large supratemporal contains anterior end of otic sensory canal and pores. Post temporal located behind lateral extrascapular. Postcranially, midabdominal, anteriorly forked, broad pelvic plates bear a posteromedian articular process. Caudal fin ray : radial ratio is 1:1.

Skull bones all heavily ornamented with closely spaced tubercles frequently anteroposteriorly elongated into short ridges on bones behind rostrum. Shoulder girdle ornamented with vertical ridges, and scales ornamented in a manner similar to the bones of head, except that some ornamentation may be convergent to rear of the scales.

Hadronector donbairdi Lund and Lund, 1984
Figs. 35–45

Previous reference.—"Short Stubby," Lund et al., in press, Fig. 1.—*Hadronector donbairdi*; Lund and Lund, 1984.

Type specimen.—MV 3635.

Referred specimens.—MV 3574 (counterpart, 3605), 3863 (counterpart, 3865), 5098, 6041, 6215. CM 27307, 27308, 30711–30713, 35537.

Horizon and locality.—Namurian A (E2B) lower Carboniferous Bear Gulch Limestone member of the Heath Formation, Big Snowy Group; south of Becket, Fergus County, Montana.

Diagnosis.—Short, stocky coelacanth, ranging in size from 28 mm to 108 mm. All external skull

Table 2.—*Proportional statistics of* Hadronector donbairdi. *Abbreviations as in Table 1.*

Statistics	$\dfrac{\text{Max. ht.}}{\text{SL}}$	$\dfrac{\text{HL}}{\text{SL}}$	$\dfrac{\text{GL}}{\text{HL}}$	$\dfrac{\text{GL}}{\text{SL}}$	$\dfrac{\text{LJL}}{\text{SL}}$	$\dfrac{\text{GL}}{\text{LJL}}$	Asp. R.
N	8	8	6	6	6	5	5
Mean	.3508	.2062	.4708	.0957	.1869	.5187	1.1884
SD	.0368	.0131	.0683	.0075	.0044	.0487	.0719
Var.	.0012	.0001	.0039	.00004	.00001	.0019	.0041

bones are heavily ornamented, ornamentation not necessarily in concordance with underlying bone pattern. Premaxilla with heavily tuberculated dorsal lamina, tuberculations grading into fine teeth along ventral margin. Small extracleithrum present in shoulder girdle. Caudal fin outline almost square cut. Proportional characters in Table 2. Meristic characters are: vert. segments, 9 cerv., 13 abd., 19–24 (mean = 21.6) caud.; P^1, 11; P^2, 3+8; D^1, 3+11; D^2, 2–3 (mean = 2.75) + 7–11 (mean = 8.25); A, 3+7–9 (mean = 8); caudal, dorsal rays, 3–4 (mean = 3.14)+18–21 (mean = 19); caudal, ventral rays, 3–4 (mean = 3.28)+17–21 (mean = 18).

Description

Hadronector is the only Bear Gulch coelacanth for which a growth series cannot be adequately demonstrated. All specimens but one range from 19–21.7 mm in head length and from 93–108 mm in standard length, are well ossified throughout, and can be presumed to represent adult specimens. CM 35537, which is unscaled and unornamented, seems to conform closely in observable features and proportions with *H. donbairdi*. It has head length of 5.3 mm and a standard length of 28 mm, although the axis is somewhat disturbed. There are no intermediate stages, indicating that alone among the Bear Gulch coelacanths, birth and growth may have taken place elsewhere than in the environments we have quarried.

Ethmosphenoid.—The ethmosphenoid moiety of the skull roof is complex, and interpretation of it is made more difficult by several factors. There is a discordance between the patterns of bones seen in mesial view and the patterns of the bones produced by growth and fusion of odontodes forming the external ornamentation. There is a discordance between the large pores midway along the transverse borders between members of anteroposterior series as seen in mesial view, and the small external pores that are seen in external view. There is also clear anteroposterior fusion of the basal bones of some
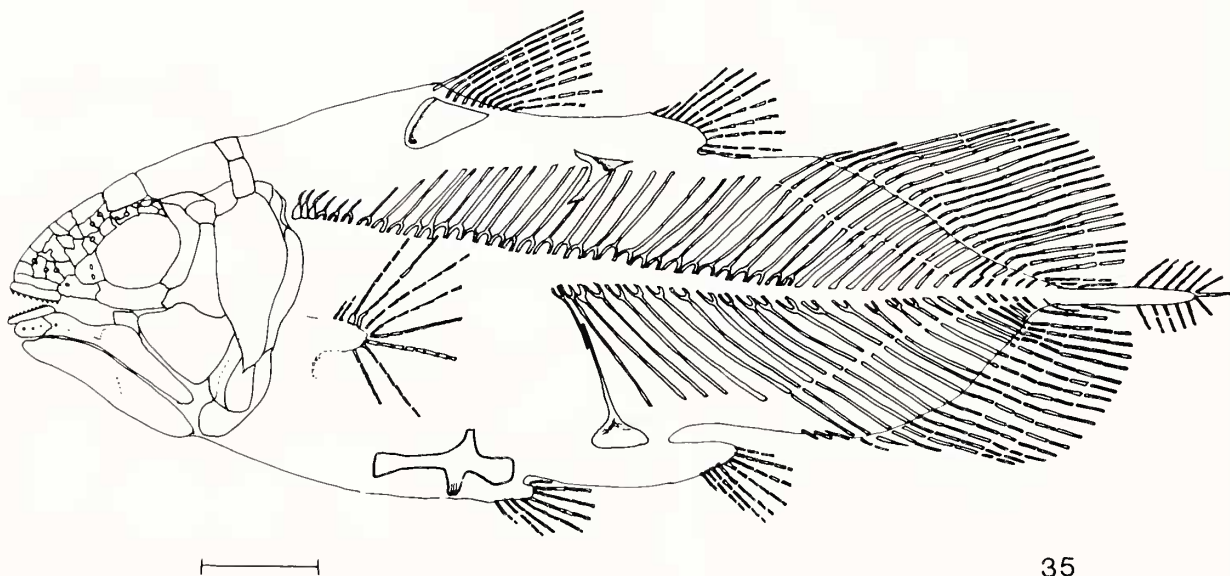

35

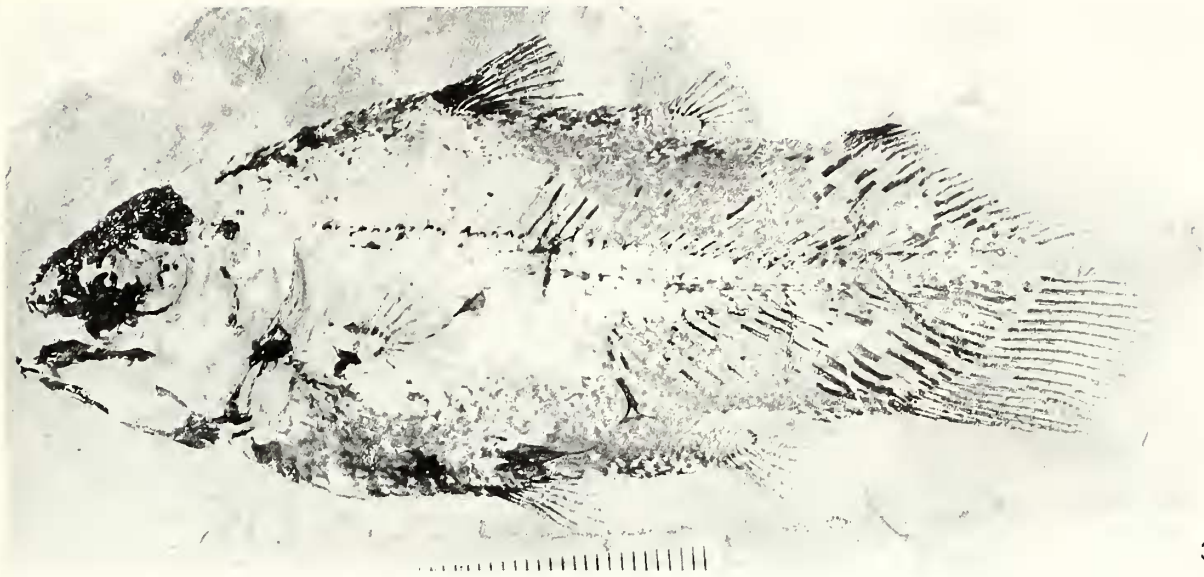Fig. 35.—*Hadronector donbairdi,* restoration based on MV 3635, CM 30723.

Fig. 36.—*Hadronector donbairdi*, Type, MV 3635. Scale is 2 mm.

members of the supraorbital and frontonasal series, which varies somewhat among individuals. Finally benzene applied to bones, which usually reveals incremental growth lines, suggests that each anterior supraorbital bone may be a binary element. Indications of an overgrown suture can be found across the narrow isthmus bridging the lateral line canal between two originally polygonal elements.

The premaxilla bears a low dorsal lamina ornamented with vertically oriented tubercles that grade into fine marginal teeth. The lamina is dorsally emarginated for two pores. Dorsally there appears to be a single anterolateral rostral. Neither premaxillae nor anterolateral rostrals meet in the midline.

The rostral series consists of six median elements, extends to the midorbital level, and is bordered posterolaterally by the parietals (Figs. 39, 42, 44). The ethmoid commissure traverses the most anterior bone of the series, the rostral. The frontonasal series, anterior to the parietals and lateral to the rostral series, is composed of six bones, one of which may be excluded from contact with a postrostral (Fig. 43). The most posterior element of this series is a product of either deep (bony) or superficial (odontode) fusion from two separate bones, and retains only marginal or near-marginal pores in superficial view. Lateral to the parietals the frontonasal series is posteriorly continuous with a series of eight small mesial supraorbital canal bones that extend back to the intracranial joint. There is particularly conspic-

uous discordance between the odontode layer and the mesial supraorbital series.

The lateral supraorbital series lies lateral to the frontonasal series anteriorly and the mesial supraorbital series posteriorly. The anterior elements each appear to have been binary elements earlier in ontogeny. There are 9 bones in the series from the rostral to the enlarged element forming the anterodorsal border of the orbit. Three lateral supraorbitals form the dorsal border of the orbit. The anterior of these is a simple bone but the posterior two are elongate and each may be product, by odontode growth and bone fusion, of four elements. There are no pores in either of the posterior two supraorbitals.

There is an additional series of three bones bordered by the anterolateral rostral anteriorly, the posterolateral rostral laterally, the antorbital posteriorly and the lateral supraorbital series mesially (Fig. 41). These bones are also notched for pores. This series is clearly shown in MV 3635 but is not evident in either CM 27307 or CM 30711 (Fig. 43).

In the infraorbital canal series, the lacrimojugal is an unusually stout element, heavily ornamented, and bears fine pores posteriorly grading into large pores near the anterior end of the bone (Figs. 37, 39, 40). Between the anterior end of the lacrimojugal and the supraorbital series lies the antorbital, perforated by one large pore without evident connection to any canal (Fig. 37). The posterolateral rostral is stout, with a prominent nasal prong anteroven-
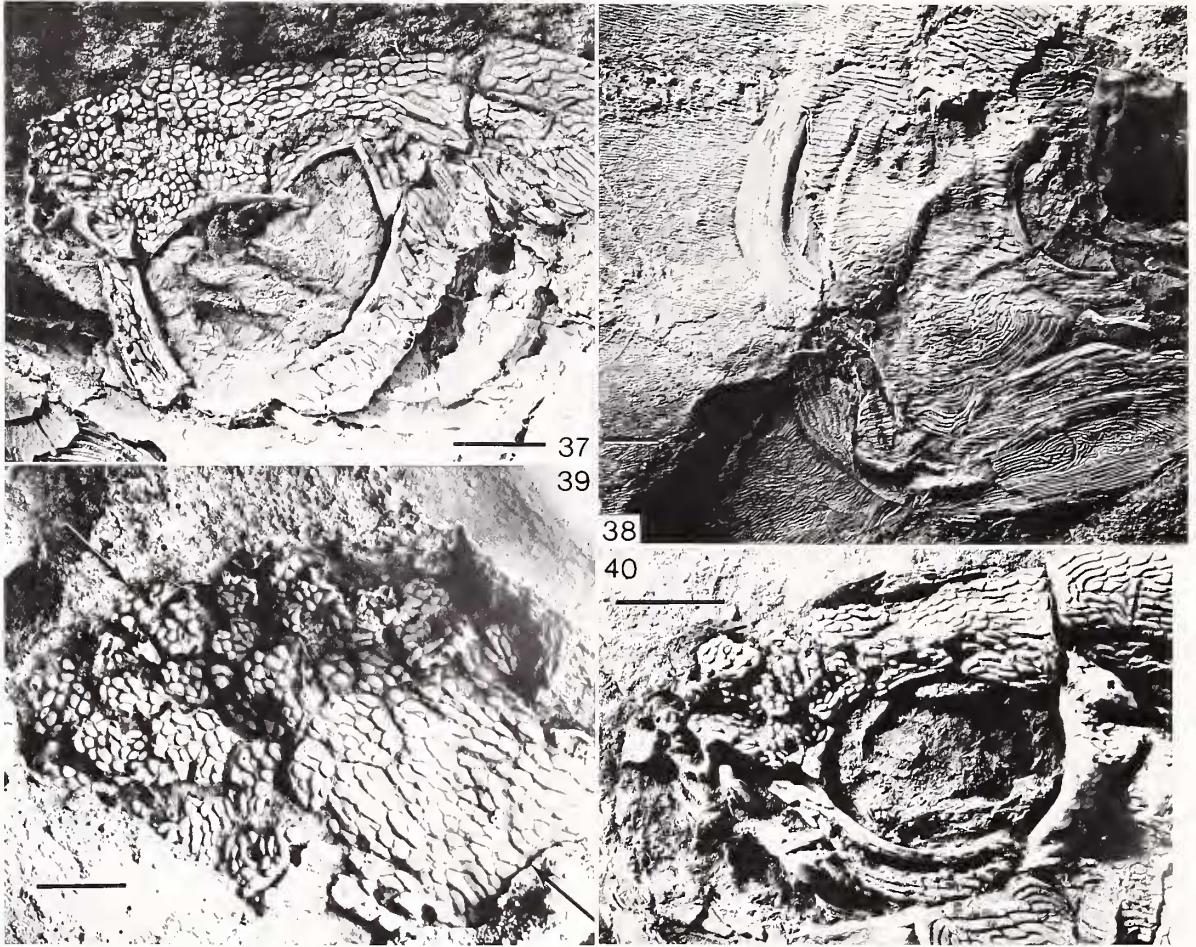
Fig. 37.—*Hadronector donbairdi,* latex peel of the external bones of the ethmosphenoid moiety, MV 3635. Scale is 2 mm.

Fig. 38.—*Hadronector donbairdi,* latex peel of the posterolateral aspect of the head of CM 27307. Scale is 2 mm.

Fig. 39.—*Hadronector donbairdi,* latex peel of the middorsal aspect of the anterior ethmosphenoid moiety of MV 6215. Scale is 2 mm; arrows indicate dorsal midline.

Fig. 40.—*Hadronector donbairdi,* latex peel of the anterolateral aspect of the head of CM 27307a. Scale is 2 mm.

trally; the numbers of pores are not clear and their pathways through the bone may have been irregular. It is not possible to determine the number of elements involved in the anterolateral rostral area, although it appears to be one bone bordered anteriorly by the premaxilla. The premaxilla itself is emarginated dorsally for two pores, and these pores as well as the number of adjoining supraorbitals support the conclusion that three elements may have been involved in the formation of the anterolateral rostral.

Clear infillings of the lateral line canals of the ethmosphenoid region are absent in *Hadronector,* but traces of infillings and relationships of the pores make it possible to indicate the path of the canals with some confidence (Figs. 41–44). Pores of the supraorbital canal do not ever seem to perforate the bones except where clear secondary fusion has occurred, and preponderantly occur along transverse lines in sets of three (Figs. 39, 44). Pores of the infraorbital canal are large but irregularly developed anterior to the lacrimojugal, the canal underlying the lateral rostral series. The supraorbital canal evidently underlay the median supraorbital series above the orbit, and may have underlain the border between the frontonasal series and the lateral supraorbital series antorbitally. A commissure between supraorbital canals almost certainly was present between rostral series bone two and three (Fig. 43). There is evidence from pore distribution that

a communicating canal exists between the supraorbital canal at the commissure and the infraorbital canal between the rostral and the anterolateral rostral (Fig. 44). There is no direct evidence on whether a separate ethmoid commissure existed at the rostral, as in *Allenypterus* (see below), *Acipenser* (Jarvik, 1948) and *Latimeria* (Millot and Anthony, 1958). It is believed, however, that the ethmoid commissure passes through the rostral, the communicating canal is the anterior lateral commissure, and the commissure between supraorbitals the antorbital commissure (Figs. 62, 75). There is no evidence in *Hadronector* for any association between the antorbital pore and any canal, nor is there any evidence for a posterior lateral commissure.

Cheek.—The cheek contains the usual compliment of postorbital, prespiracular, tall squamosal, quadratojugal and preoperculum, all but the prespiracular heavily ornamented, and tightly fit together (Figs. 40, 43). The infraorbital lateral line canal is joined by the jugal canal at the lacrimojugal-postorbital-squamosal boundary and is continued through the anterior margin of the postorbital. The anterior margin of the postorbital is level with the intracranial joint. Ornamentation of the postorbital is in the form of large posteriorly projecting serrations, and fine pores can be found between the bases of these serrations. The jugal canal is short and curves ventrally into the preopercular canal; no extension or pores occur dorsal to this junction although fine pores occur ventrally through the preoperculum. The quadratojugal pit line is prominent, extending from the dorsal half of that bone into the ventral aspect of the squamosal almost to the jugal canal (Fig. 40). The prespiracular is thin and appears flexible, and bears no trace of a canal. The suboperculum is much smaller than the operculum, and both bones are heavily ornamented.

Oticooccipital.—The oticooccipital moiety of the skull roof consists of large paired postparietals flanked laterally by moderate sized supratemporals and tabulars that gradually expand posterolaterally (Figs. 39, 43, 44). The posterior border of each supratemporal has a concave suture for the reception of the anterior end of the tabular. Three extrascapulars border the posterior margin of the skull roof. The infraorbital lateral line canal emerges from the anterodorsal end of the postorbital bone lateral to the anterior edge of the supratemporal. The otic canal continues through the supratemporal and tabular into the lateral extrascapular, where the supratemporal commissure branches off. Pores above the
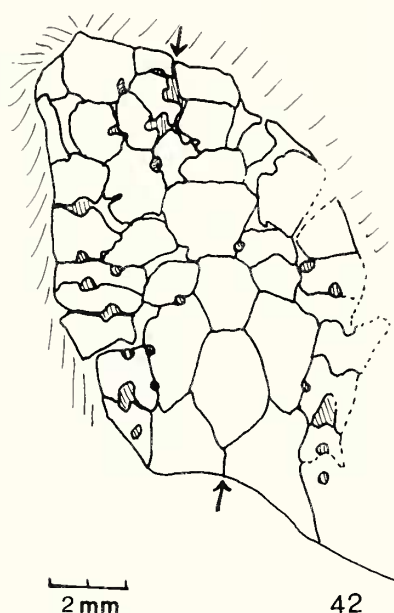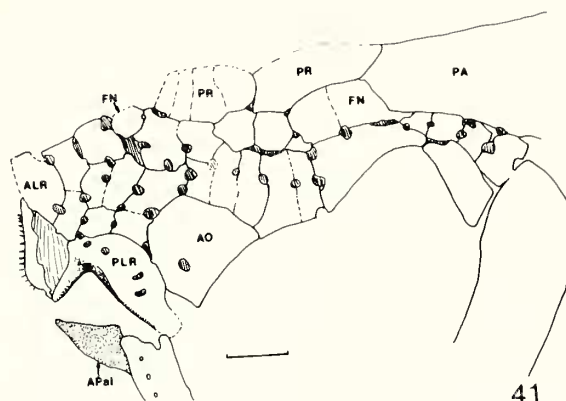
Fig. 41.—*Hadronector donbairdi*, reconstruction of bones of the snout of MV 3635. See Fig. 37.

Fig. 42.—*Hadronector donbairdi*, reconstruction of the bones of the middorsal aspect of the ethmosphenoid moiety of MV 6215. Scale is 2 mm. See Fig. 39.

otic canal are few and large, whereas pores immediately posterior to the supratemporal canal are numerous and fine. T-shaped pit lines are usually prominent anterior to the middle of each postparietal, although the posterior pit line may be less prominent (Figs. 37, 38, 40). The anterolateral margin of the tabular forms the posterior wall of the spiracle.
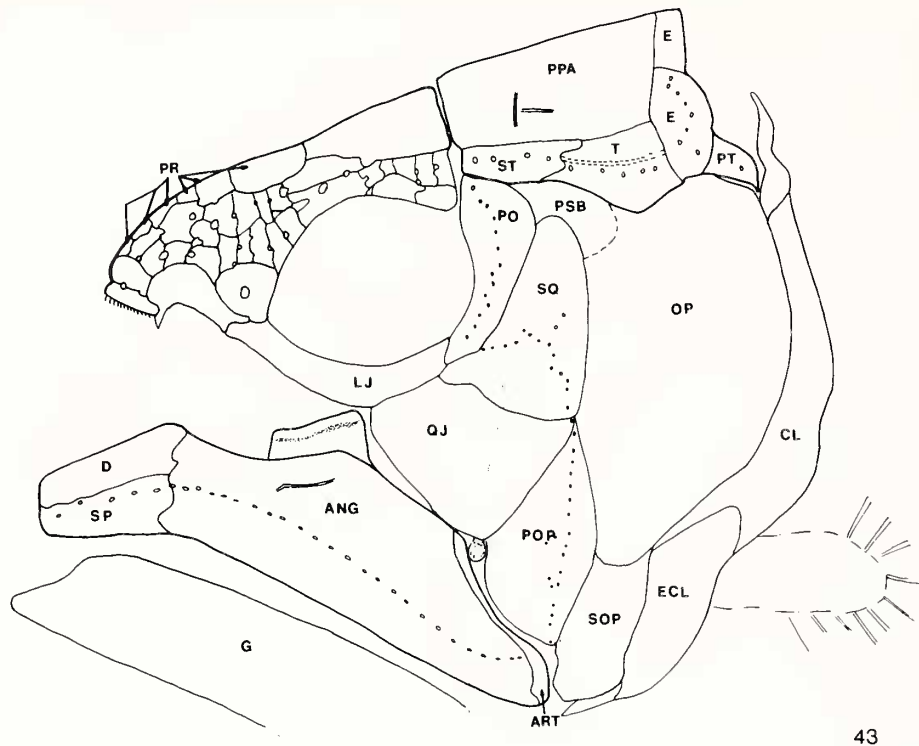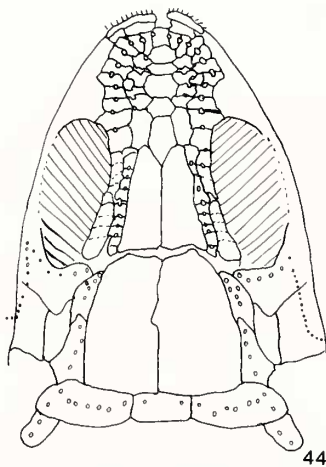
Fig. 43.—*Hadronector donbairdi*, restoration of the external bones of the head in lateral view, based on MV 3635 and CM 27307.
Fig. 44.—*Hadronector donbairdi*, restoration of the external bones of the head in dorsal view, based on MV 6215 and 3635.

Palate, lower jaw, and branchials.—The anterior end of the palate is marked by a small but strongly ossified triangular autopalatine, faced ventrally with a toothbearing dermoplatine and anterolaterally by a fringe of small toothplates. There is a short ectopterygoid posteriorly (Fig. 45). The metapterygoid appears to be short and stout. Posteroventral to the extensive endopterygoid, the quadrate is strongly convex anterior to the articular condyle and ventral to the body of the endopterygoid. The palate is ornamented by concentric rings of fine denticles, the center being close to the quadrate (Fig. 45). The
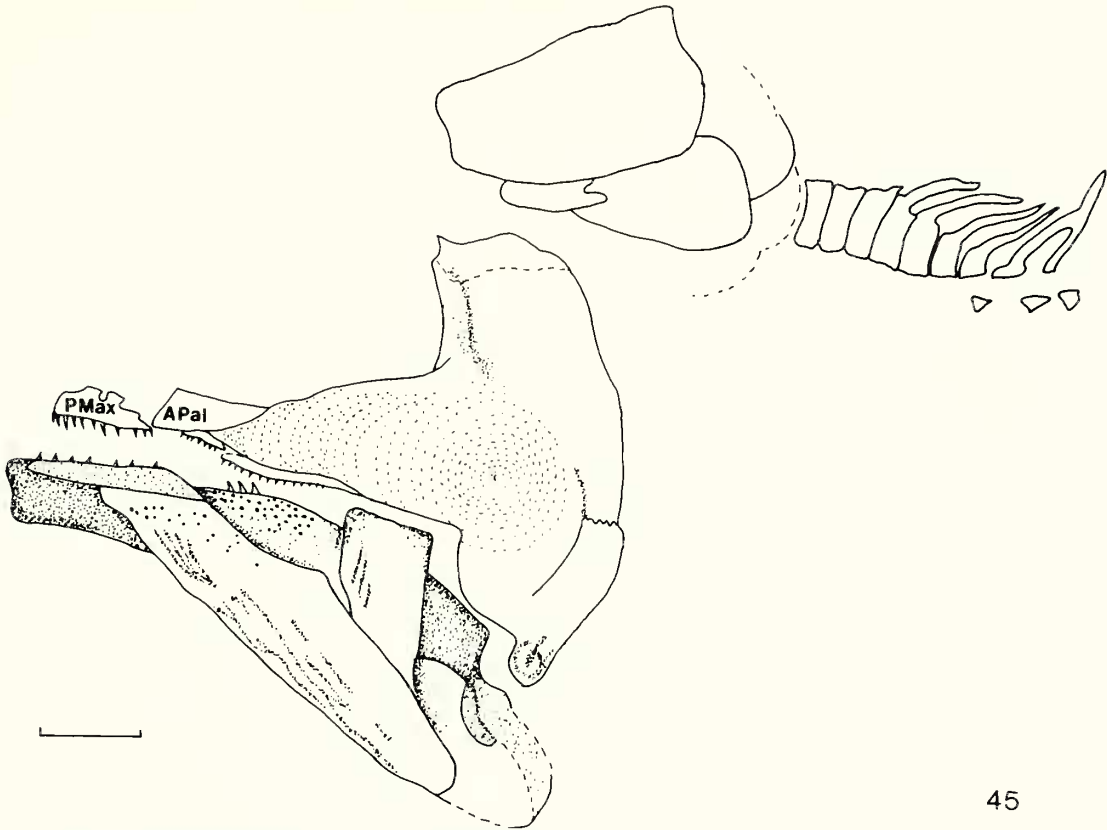
Fig. 45.—*Hadronector donbairdi*, internal view of the palate and lower jaw, with cervical neural arches. Based on MV 6041 and CM 27307. Scale is 3 mm. Abbreviations: APal, autopalatine; PMax, premaxilla.

palate articulates with the relatively short antotic process mesial to the anterodorsal edge of the postorbital bone. There is no evidence of a basipterygoid process.

The oral margin of the dentary and the associated splenial are oriented at a strong angle to the long axis of the lower jaw, and are quite short. There is a strong dorsal concavity at the anterior end of the angular before it rises to the coronoid eminence. At the posterior end of the angular, a distinct difference in ornamentation signifies that the posterior end of the ossification in Meckel's cartilage projects beyond the angular (Fig. 38). Large pores mark the course of the mandibular canal through the splenial and the anterior end of the angular, followed by fine pores posteriorly. The path of the pores of the mandibular canal curves dorsally below the articulation to meet the preopercular canal. There is a strong pit line in the angular immediately below the coronoid. The entire lateral aspect of the lower jaw is strongly ornamented (Fig. 38). The dentary bears a series of small teeth along its oral margin.

Mesial to the dentary can be seen a number of thin plates bearing small denticulations, extending over the anterodorsal end of the prearticular (Fig. 45). A large precoronoid extends to the coronoid, apparently abutting against it immediately mesial to the dorsal margin of the angular. The coronoid is quadrangular and sets upon the dorsal edge of the prearticular. The prearticular extends posteriorly to the level of the articular condylar fossa. Details of the retroarticular region are not preserved.

The branchial arches of *H. donbairdi* are unknown.

Shoulder girdle.—The postemporal is small, does not contact the tabular, and is closely associated with the anocleithrum-cleithrum contact. The anocleithrum bears a slightly S-shaped dorsal process. The cleithrum is long, with a short shaft connecting it to the relatively short clavicle, and the pectoral fin axis must have emerged somewhat lower on the flank of *Hadronector* than in any other Bear Gulch coelacanth (Fig. 40). The extracleithrum therefore, is also short, and is usually overlapped ventrally by

the suboperculum. The cleithrum and extraclei-thrum are ornamented by strong, sharp vertical ridges.

Postcranial skeleton.—The first three postcranial neural arches are broadly in contact with each other and bear only slight median crests. The following four arches have successively shorter broad ventral extremities, and still lack significant neural spines. The eighth neural arch has a slightly broadened "footplate," and bears a short neural spine (Fig. 45), as do the succeeding two neurals. The following three neurals, under the first dorsal fin plate, increase in height posteriorly, and the remaining 10 neurals in the abdominal region are of normal height (Figs. 35, 38). The precaudal segments of *H. donbairdi* there-fore consist of nine shortened, cervical neurals and only 13 abdominals. The stem of the second dorsal fin plate intercalates between the last two abdominal neural spines and bears an expanded, thin plate that is well ossified only along its ventral margin (Figs. 35, 36). The stem of the anal plate is supported below the first haemal spine and against the first full length haemal spine, and bears an anteroposteriorly elongated basal plate.

The pelvic plate resembles that of the rhabdoder-matids and coelacanthids, bearing an anterolateral and anteromesial spur as well as a strong posterior median articulatory process interdigitating with the contralateral pelvic plate (Fig. 35).

An ossified swim bladder is present.

All median and paired fins are composed of well spaced and articulated fin rays, which are orna-mented. Axial elements of the fins leave vague impressions, but were not ossified.

Genus *Polyosteorhynchus* Lund and Lund, 1984

Type species.—*Polyosteorhynchus simplex* Lund and Lund, 1984.

Diagnosis.—Dorsal margin of premaxilla emar-ginated for one or more pores and bears few, large teeth. Rostral bone small, postrostrals either very small or absent. Nasal-frontal-parietal series not bi-laterally symmetrical and there are no enlarged, clearly defined "parietal" bones. Lateral and mesial supraorbital series unmodified by fusion. Anterior end of otic canal passes between postparietal and supratemporal. Anterior end of postorbital slightly behind intracranial joint, and squamosal may be present as one or two bones. Pelvic plates long, nar-row, do not bear a posteromedian articular process, and are midabdominal. Caudal fin ray ratio is 1:1.

Polyosteorhynchus simplex Lund and Lund, 1984
Figs. 46–56

Previous reference.—"Big Head," Lund et al., in press, Fig. 1.—*Polyosteorhynchus simplex* Lund and Lund, 1984.

Type specimen.—MV 6043.

Referred specimens.—MV 2946, 3591, 6042. CM 27283, 30597, 30714, 35540.

Horizon and locality.—Namurian A (E2B), Low-er Carboniferous Bear Gulch limestone member of the Heath Formation, Big Snowy Group; south of Becket, Fergus County, Montana.

Diagnosis.—Moderate sized coelacanth, ranging from 35 mm to an estimated 186 mm in standard length, and maximum height occurring midway be-tween rear margin of head and origin of first dorsal fin. Bones of the skull relatively thin and orna-mented with coarse, low, flat topped tubercles or ridges, although anterior bones of ethmosphenoid region sparsely ornamented and premaxilla devoid of ornamentation. Premaxilla bears 3–4 large teeth. Bones of cheek deeply overlapping. Extracleithrum large. Caudal fin outline almost square cut in larger specimens. Proportional characters given in Table 3. Meristic characters: vert. segments, 8–9 cerv., 23–24 abd., 25–26 caud.; P^1, 8–9; P^2, 12; D^1, 7; D^2, 14; A, 12–16; caudal, dorsal rays, 3–4+14–15; caudal, ventral rays, 3–4+14–16.

Description

Specimens of *P. simplex* are uncommon in the Bear Gulch coelacanth fauna, with only five com-plete measurable individuals. The largest, CM 30597, lacks a head but is complete from the rear margin of the operculum and shoulder girdle to the tip of the median caudal lobe; its length has been estimated on the basis of the proportions of the complete specimens (Fig. 73).

Two specimens, CM 35540 (Fig. 48) and MV 3591, measure 35 mm in standard length. CM 27283, with a middorsal skull length of 20 mm, is roughly estimated to be 86 mm in standard length. The spec-imens provide remarkably good information on morphological changes with growth. Ornamenta-tion is not present on the smaller specimens, and is represented by few sparse tubercles on the postpari-etals and the parietal region and few, coarse ridges on the angular and gular of CM 27283 (Fig. 52). The angular of the two smallest specimens is very low relative to its height and the height of the cor-onoid bone, only approaching adult proportions in

Table 3.—*Proportional statistics of* Polyosteorhynchus simplex. *Abbreviations as in Table 1.*

Statistics	$\dfrac{\text{Max. ht.}}{\text{SL}}$	$\dfrac{\text{HL}}{\text{SL}}$	$\dfrac{\text{GL}}{\text{HL}}$	$\dfrac{\text{GL}}{\text{SL}}$	$\dfrac{\text{LJL}}{\text{SL}}$	$\dfrac{\text{GL}}{\text{LJL}}$	Asp. R.
N	2	4	5	4	4	5	3
Mean	.3314	.2288	.3895	.0934	.1801	.5067	1.133
SD	—	.0165	.0905	.0184	.0333	.0609	.2309
Var.	—	.0002	.0065	.0002	.0008	.0029	.0355

CM 27283 (Figs. 5, 6). The outline of the caudal fin changes from elliptical in the small specimens to square cut by 105 mm (MV 6042) (Figs. 47, 48), and the median caudal lobe seems reduced to a virtual vestige at the largest size. As in all coelacanths reported on here, the number of caudal neural and haemal spines increases with absolute size as a result of increased ossification.

Ethmosphenoid.—The ethmosphenoid moiety of the skull roof consists of three paired series of small bones, the parieto-fronto-nasal series nearest the midline, and the mesial and lateral supraorbital canal bones (Figs. 50, 53). The bones normally termed parietals in coelacanths, namely the first paired elements anterior to the intracranial joint, that usually bridge the orbital region, are, in *Polyosteorhynchus,* produced by fusion during ontogeny of two bones in anteroposterior series. The anterior member, however, bears a strong anteroventral ethmoid lamina (Fig. 52). While there are usually five elements in the parieto-nasal series, the precise arrangement and proportions of these are variable from specimen to specimen as well as across the dorsal midline.

The mesial supraorbital series, consisting of 12 to 13 thin elements, evidently overlaid the supraorbital lateral line canal; each bone emarginated mid-

way along the anterior and posterior borders for a large lateral line canal pore. The mesial supraorbital series of each side meets at the dorsal midline anterior to the parieto-nasal series in a manner strongly resembling the antorbital commissure of *Allenypterus* (Fig. 62) and *Hadronector* (Fig. 41). There are no clear indications of a median series of rostrals and postrostrals.

The lateral supraorbital series contains an element of uncertain shape overlying the antotic process and anterior to the dorsal end of the postorbital, continuous with the remainder of the series. From this element to the midpoint of the orbit, the bones of the series decrease in height and increase in width. Only two lateral supraorbitals occupy the antero-dorsal corner of the orbit. The lateral supraorbital series continued as a series of seven to eight bones to the anterior part of the dorsal midline. The most anterior "orbital" supraorbital is bordered by the small antorbital ventrally and by a supplemental lateral ossification anteriorly (Fig. 53). This supplemental ossification (see *Allenypterus,* Fig. 60) overlays the antorbital-posterolateral rostral joint.

The infraorbital canal bones consist of the lacrimojugal, the posterolateral rostral and two or three anterolateral rostrals, bordered by the premaxilla

46
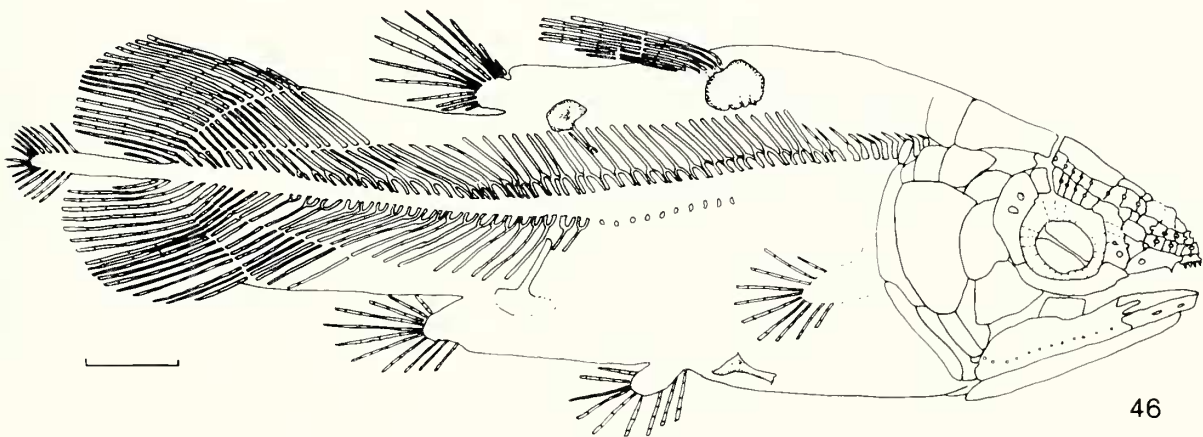
Fig. 46.—*Polyosteorhynchus simplex,* restoration based on MV 2946, 6042 and 6043.
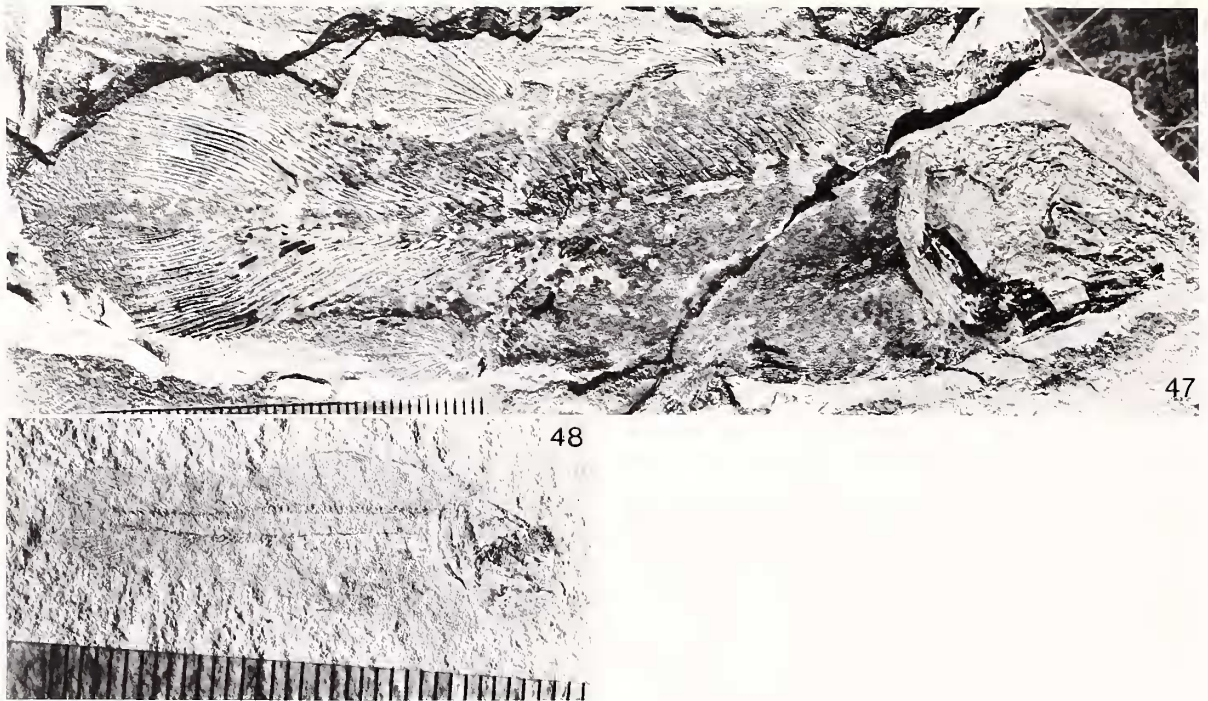
Fig. 47.—*Polyosteorhynchus simplex*, type, MV 6043. Scale in mm.
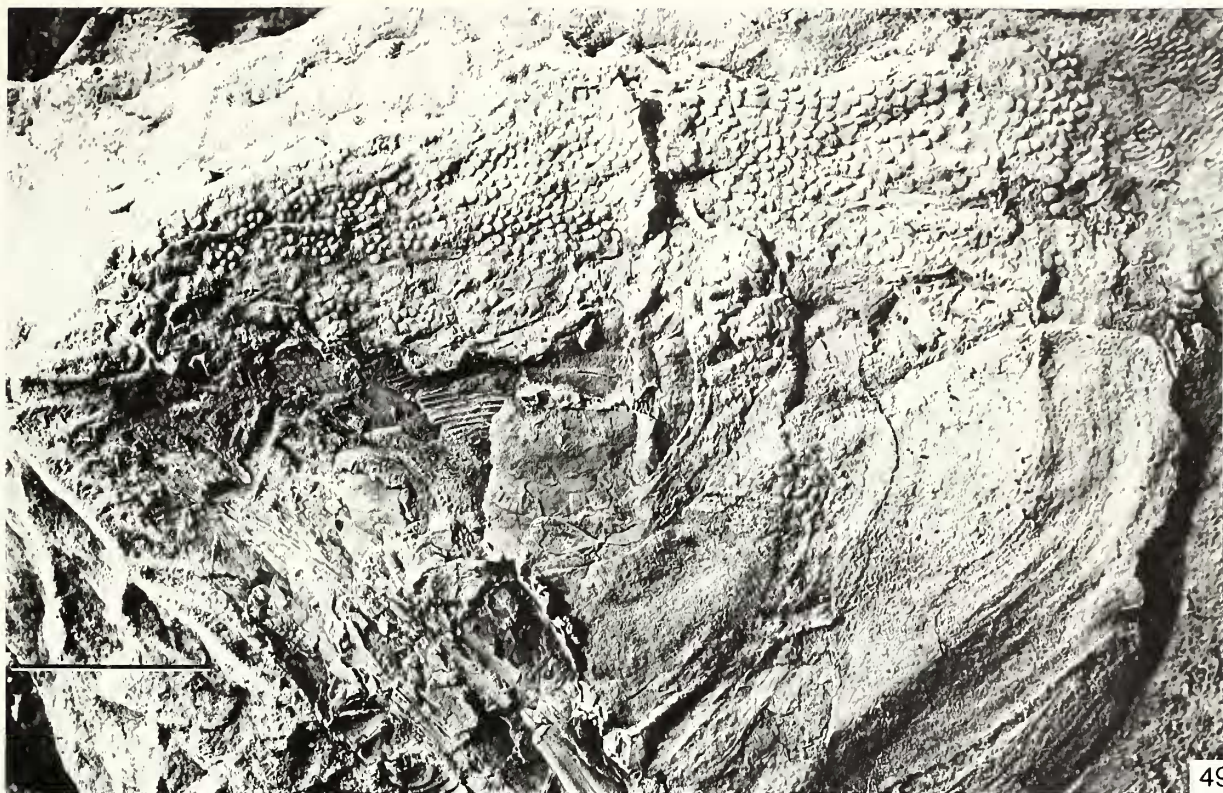Fig. 48.—*Polyosteorhynchus simplex*, CM 35540. Scale in mm.

ventrally. The anterior pores of the infraorbital canal, or ethmoid commissure, are located between anterolateral rostrals and the premaxilla. There is a suggestion in CM 6042 of a very small element that could possibly be a median rostral.

The lateral line canal pattern of the ethmosphenoid moiety is essentially as in *Allenypterus montanus,* as far as can be determined from the few available specimens. There is clearly an antorbital commissure between supraorbital canals at the anterior end of the naso-fronto-parietal series, and most probably an anterior communicating canal between the canals at the anterior end of the lateral rostral series. There also appears to be a posterior lateral commissure between infraorbital and supraorbital canals, passing posterodorsally in front of the antorbital and either joining or ending in close proximity to the supraorbital canal at the most anterior "orbital" lateral supraorbital bone.

Cheek.—All bones of the cheek except for the postorbital are thin, heavily overlapping, and lightly ornamented with low pustules. The cheek bones except the postorbital also show circumferential growth lines of the basal lamellar layer, and most unusually, a central zone between the external ornamented zone

and the lamellar basal bone. This highly textured zone is only typical of coelacanth and other sarcopterygian scales. A large quadratojugal bears scattered pits of the quadratojugal pit line and overlaps the tall, narrow preopercular enough to prevent accurate determination of the course of the preopercular canal. The preopercular canal in the squamosal rises to the vicinity of a large pit as in *Rhabdoderma elegans* (Fig. 6), and is met by the jugal canal ventral to the middle of the bone (Fig. 49). CM 6043, however, is conspicuously different from any other known coelacanth as well as other specimens of *P. simplex* in having a dorsal and ventral squamosal element. The ventral element carries the jugal and the ventral ramus of the preopercular canals, while the dorsal squamosal is, as far as can be determined, without either lateral line canal or pit line (Fig. 51). The significance of this difference is unclear, in view of the scarcity of specimens.

The operculum is tall, tapers ventrally, and is conspicuously ornamented in larger specimens with a concentric pattern of stout pustules (Fig. 51). It does not articulate directly with the tabular. The suboperculum is fitted around the ventral end of the operculum, is tall, narrower dorsally than ventrally,

Fig. 49.—*Polyosteorhynchus simplex*, latex peel of the head of MV 6042. Scale is 5 mm.
Fig. 50—*Polyosteorhynchus simplex*, latex peel of the anterior part of the head of MV 6043. Scale is 2 mm.
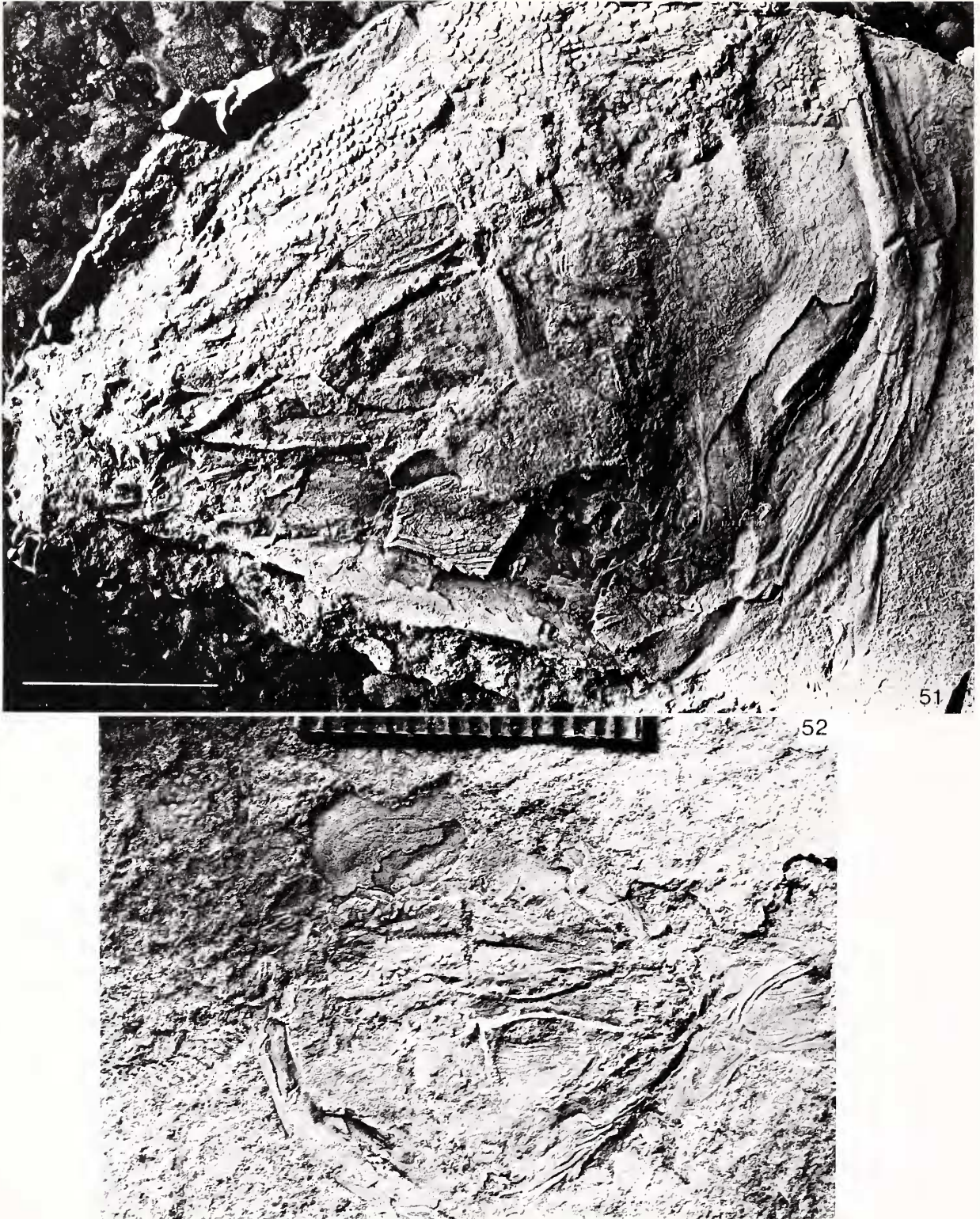
Fig. 51.—*Polyosteorhynchus simplex*, latex peel of the head of MV 6043. Scale is 5 mm.
Fig. 52.—*Polyosteorhynchus simplex*, latex peel of the head of CM 27283. Scale in mm.

and curves slightly forward under the posteroventral margin of the preoperculum. It is ornamented, as is the operculum, with stout pustules. The operculum and suboperculum are overlapped by the squamosal and preoperculum, and in turn usually completely overlap the shoulder girdle.

Oticooccipital.—The oticooccipital moiety of the skull roof consists of large postparietals flanked laterally by relatively wide supratemporals and tabulars and posteriorly by three extrascapulars (Fig. 49). There are no pores in the supratemporal; the otic canal passes between the anterior end of the supratemporal and the postparietal, leaving a prominent gap. The otic canal enters the tabular at its anteromesial contact with the supratemporal-postparietal suture and traverses the bone close to this suture, apparently giving off very fine pores. The anterolateral edge of the tabular forms a conspicuous, descending posterior wall of the spiracle, and there is reason to suspect that there is some fusion of this descending lamina with the posterolateral wall of the braincase (Fig. 49). An anterior pit line emerges onto the postparietal at the posterior end of the supratemporal gap (Fig. 49) and trends posteromesially. There is a space posterior to the end of this pit line, and a posterior pit line mesial to the rearward projection of the anterior pit line extends virtually to the posteromesial corner of the postparietal. There is some suggestion in CM 27283 of a lateral flange of the anterior end of the postparietal extending underneath the supratemporal and anterior part of the otic canal (Fig. 52). The postparietals are weakly joined in the midline.

Palate and lower jaw.—The palate is of typical coelacanth shape (Fig. 52) with an unusually wide metapterygoid region and stout epipterygoid process. A fringe of anterior dermopalatine teeth may be seen in front of the autopalatine. The ectopterygoid and the ventral edge of the endopterygoid to the quadrate bear few, relatively stout tubercles. The anterodorsal quadrant of the endopterygoid bears fine denticulated ridges, while the remainder of the endopterygoid and metapterygoid bear randomly oriented, fine denticulations (Fig. 49).

Few details of the lower jaw of *Polyosteorhynchus* are noteworthy, aside from the developmental information noted above (Fig. 56). The diastema of the jaw is small and relatively inconspicuous, rendered further so by the line of the precoronoid posterior to the end of the dentary. Many fine teeth on the anterolingual portion of the jaw seem to be borne upon a single plate. The prearticular is extensive,

supports the coronoid, and bears longitudinal rows of denticulated ridges. The coronoid is quadrangular and seems to lack the prominent "saddle" seen in Rhabdodermatidae. There is a conspicuous projection of the lateral surface of the retroarticular posterior to the end of the angular, and there clearly are separate retroarticular and articular ossifications in CM 27283. These are not distinguishable in large specimens (Figs. 52, 56).

Although the smallest specimens show relatively well ossified gill arches, no details can be resolved aside from the observation that the branchial skeleton is not obviously different than that of other coelacanths from the Bear Gulch limestone.

Shoulder girdle.—The anocleithrum bears a stout spike-like vertical process, and seems to be tightly associated with the posttemporal (Fig. 51). The dorsal portion of the cleithrum is relatively short, weakly ornamented with vertical ridges, and bears a long anteroventral process articulating with the long dorsal arm of the clavicle. The clavicles are loosely associated in the ventral midline. The ventral ends of the clavicles are sturdily ossified and expanded. The extracleithrum is extensive and heavily ornamented. The articular process of the scapulocoracoid is ossified and projects beyond the extracleithrum-cleithrum junction but details cannot be resolved (Fig. 51).

Postcranial skeleton.—An ossified swim bladder is present, as in every well preserved coelacanth.

The anterior seven to eight neural arches have laterally expanded bases; the first three bear only slight median crests. The following four to five arches bear strongly inclined, short neural spines. Postcranial neural arches nine and ten assume the narrow lateral aspect typical of those that follow while having neural spines inclined at the same angle to the vertical as the following abdominal arches. These spines are short, however. The succeeding four neural spines underlie the first dorsal fin plate and are slightly shorter than those of the remainder of the column (Fig. 46).

The pelvic plates are small, elongate and thinly ossified, without medial articulatory processes. The pelvic plates of CM 30597 are proportionately considerably longer than in MV 6043, but show no additional details.

Genus *Allenypterus* Melton, 1969

Type species.—*Allenypterus montanus* Melton, 1969.
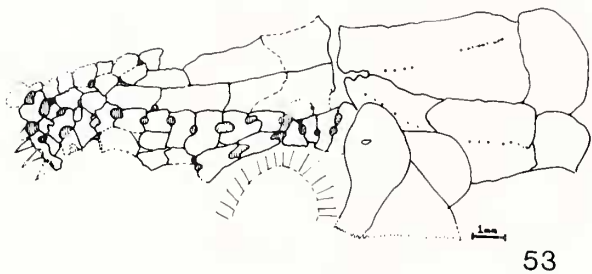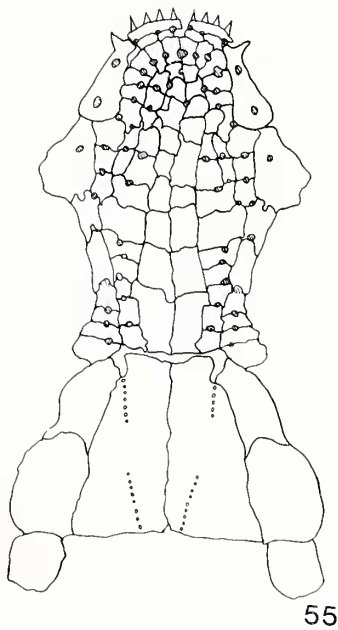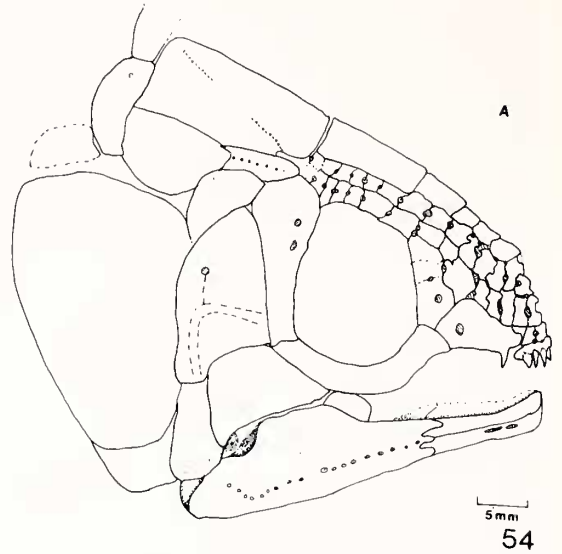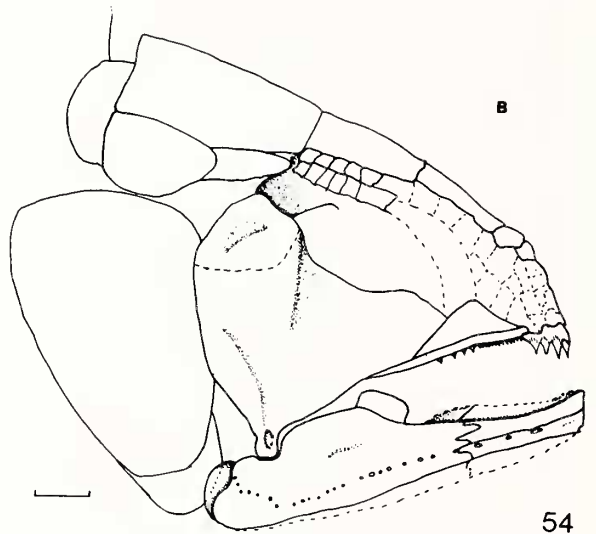
Fig. 53.—*Polyosteorhynchus simplex,* reconstruction of the bones of the ethmosphenoid moiety of MV 6043. See Fig. 50.
Fig. 54.—*Polyosteorhynchus simplex,* A, restoration of the lateral view of the head, based on MV 2946, 6042, 6043; B, restoration of the palate, based on MV 2946, 6042, CM 27283.
Fig. 55.—*Polyosteorhynchus simplex,* restoration of the skull in dorsal view, based on MV 6042, 6043, CM 27283.

Revised diagnosis.—Premaxilla narrow, apparently unperforated and unemarginated, and bears a row of fine teeth. Median rostral and one postrostral both small and rostral possibly a fusion product. Mesial supraorbital series overlies lateral line canal and fuses relatively late in ontogeny with mesial skull bone series, resulting in a pored and canal bearing nasal-frontal-parietal series and an unmodified lateral supraorbital series. Several supplementary canal bones present between anterior supraor-

bital canal series dorsally and lateral rostral bones ventrally. Anterior end of otic canal passes beneath postparietal-supratemporal suture. Posttemporal in contact with posterolaterally expanded tabular. A median ventral row of thick scales between clavicles and pelvic girdle. Pelvic plates are high triangles that do not articulate in the ventral midline, and are located near rear of peritoneal cavity. Dorsal lobe of caudal fin originates anterior to level of first caudal segment, is elongate and has a fin ray : endo-

skeletal support ratio greater than 1:1. Fin rays and length of the ventral caudal lobe greatly reduced and have a 2:1 ratio to endoskeletal supports. "Median" caudal lobe bears no terminal fin rays.

Discussion.—*Allenypterus montanus* was originally described (Melton, 1969) as an actinopterygian of the family Dorypteridae. In all characteristics of cranial and postcranial morphology, except for the body form, *A. montanus* is clearly a coelacanth. The body form is unique among known coelacanths.

Allenypterus montanus Melton
Figs. 57–66

Previous references.—*A. montanus* Melton, 1969.
A. montanus, Glickman, 1977.
A. montanus, Lund et al. (in press).
A. montanus, Lund and Lund, 1984.

Type specimen.—MV 2555.

Referred specimens.—CM 27284–27288, 30627, 30628, 30716, 35200, 35202, 35363, 35538, 35539, 37509. MV 2771, 2920, 2949, 3640, 4736, 5381, 5382, 5549, 5550, 6216, 6217, 6937, 6938.

Horizon and locality.—Namurian A (E2B) Lower Carboniferous Bear Gulch Limestone member of the Heath Formation. Big Snowy Group, south of Becket, Fergus County, Montana.

Revised diagnosis.—Highly compressed, dacriform coelacanth with extended epichordal caudal fin and reduced hypochordal caudal. Body maximum height at origin of first dorsal fin, slopes downward from second dorsal fin to short, rayless median lobe. Epichordal caudal extends from close behind second dorsal to start of median lobe as series of short well articulated rays of uniform height. Size range from 32 mm to 152 mm standard length. All external bones of skull heavily ornamented with broad, flat topped ridges except premaxilla. Seven lateral supraorbitals over orbit, the most posterior two of which fuse, and five antorbitally. Bones of cheek thin, deeply overlapping each other, opercular series and rear of lower jaw. Meristic characters: vert. segments, 8 cerv., 20–21 abd., 36–44 caud.;
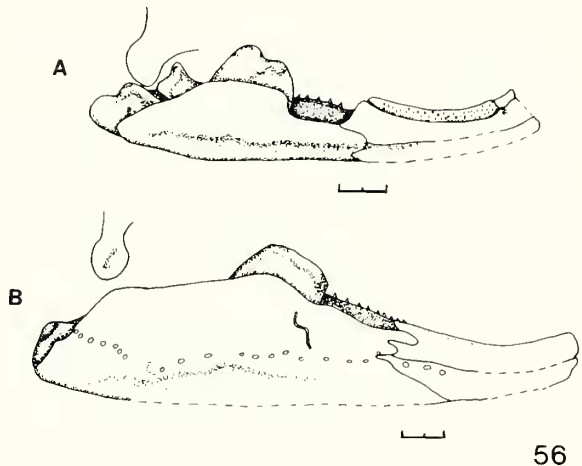
Fig. 56.—*Polyosteorhynchus simplex,* lower jaws. A, from CM 27283; B, based on MV 2946. Scale is 2 mm.

P^1, 6–7; P^2, 6–7; D^1, 2–3+11–14; D^2, 6–9; A, 6–7; caudal, dorsal rays, 3–4+55–69; caudal, ventral rays, 15. 6–9 scales in median ventral scale shield. Proportional characters given in Table 4.

Description

The body shape of *A. montanus* is unique among known coelacanths (Fig. 57). All other known coelacanths are approximately round in transverse section and relatively uniform in body height from the rear of the skull to the origin of the diphycercal tail. *A. montanus* is strongly compressed, with a short, high head and trunk, long asymmetrical tail with a dominant epichordal lobe, and a straight ventral outline. The median caudal lobe characteristic of coelacanths lacks a terminal tuft of fin rays and is rarely preserved; most specimens appear to have had the terminal bitten off, approximately at the level of the last few epichordal rays. Only four specimens are complete (Fig. 58). The smallest individuals show little of the dacriform outline of the adults; growth parameters are best fit by straight lines and maximum height increases most sharply in relation

Table 4.—*Proportional statistics of* Allenypterus montanus. *Abbreviations as in Table 1.*

Statistics	Max. ht. / SL	HL / SL	GL / HL	GL / SL	LJL / SL	GL / LJL
N	11	11	4	4	4	4
Mean	.3598	.1874	.3598	.0666	.1434	.4567
SD	.0382	.0161	.0356	.0078	.0093	.0259
Var.	.0013	.0002	.0009	.0004	.00006	.0005

57
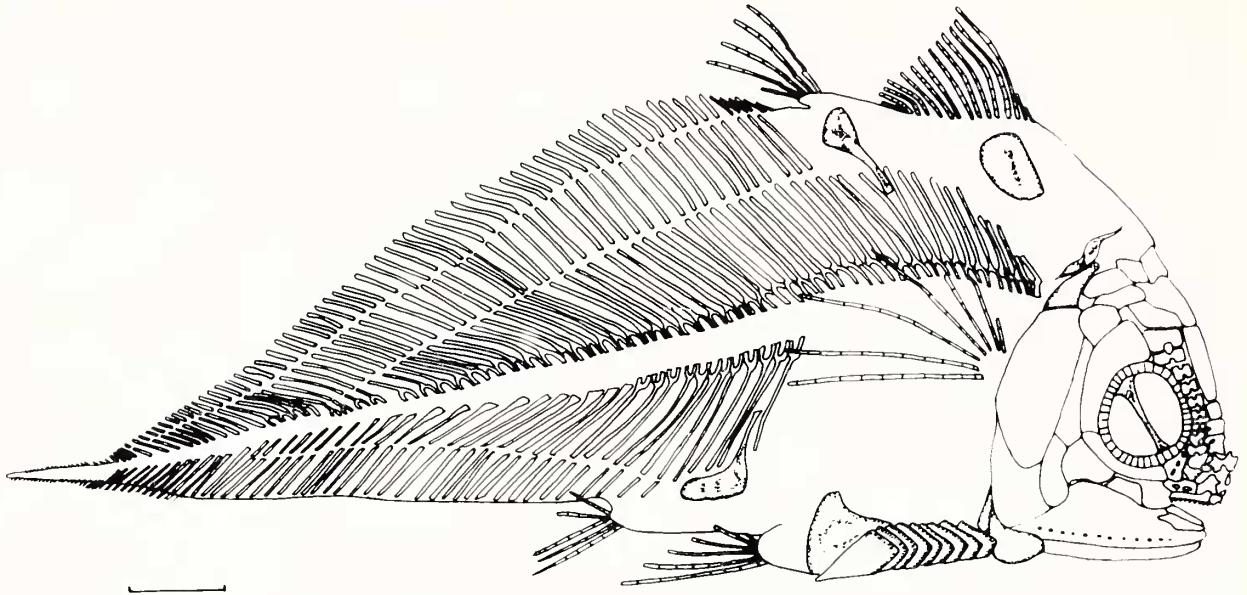
Fig. 57.—*Allenypterus montanus,* restoration based on MV 5381, CM 37509. Scale is 1 cm.

to linear parameters around the head (Fig. 58). Linear parameters of head length to body length are virtually identical in slope to those of the other accurately measureable coelacanths in the Bear Gulch limestone (Fig. 72).

Ethmosphenoid. — The ethmosphenoid moiety of the skull roof of the largest individuals consists of

58
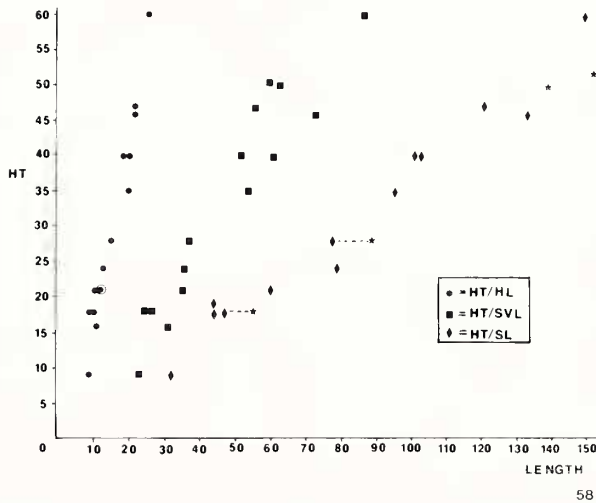
Fig. 58.—*Allenypterus montanus,* graphs of height/head length (HT/HL), height/snout–vent length (HT/SVL), and height/standard length (HT/SL). Stars indicate total length measurements on specimens with terminal lobes.

a median rostral separated in the midline from a median postrostral, three to four paired frontonasals often asymmetrical and often accompanied by a peripheral frontonasal (Fig. 61), paired parietals, and a lateral supraorbital series, all of which are ornamented with anteroposteriorly oriented but basically circumferential flat topped ridges (Fig. 65). The nasal-frontal-parietal series bears pores that correspond with the marginal pores laterally in the supraorbital series. Pores of the supraorbital canal in the largest individuals tend to be subdivided anteroposteriorly and in places to be isolated from the margins of the bones, evidently by late growth of bone or ornamentation (Figs. 65, 66). Specimens of somewhat smaller size, such as CM 30627, and internal views of larger individuals usually reveal the calcite filled supraorbital canal in a wide space between the pore-free parietals and the well formed lateral supraorbitals (Fig. 64). Ossifications dorsal to the supraorbital canal are present, and are clearly similar to the supraorbital series in MV 6216. It can only be concluded that the bones of the nasal-frontal-parietal series of adults are each the result of the fusion of mesial supraorbital canal bones with the anamestic bones more mesiad. Thus the position of each pore in the parietals, the frontonasals, the most posterior, lateral supraorbital and possibly even the rostral, may mark the former location of a transverse suture between two elements (Fig. 61).

Fig. 59.—*Allenypterus montanus.* CM 37509a. Scale in mm.

There are indications from the three-dimensionally preserved head of MV 2555 that the lateral supraorbitals did indeed lay more on the lateral aspect of the living fish, while the more mesial bones faced dorsally. The two series of bones would then have been positioned almost at right angles to each other and to the lateral line canal. There may have been strong structural advantages to the fusion of the mesial supraorbital series with the parietal series.

Filling of the supraorbital canal itself by calcite clearly shows, in CM 27286 and MV 5381, that there was a commissure between supraorbital canals at the level of the last postrostral, as is also suggested by the pattern of the pores in the surrounding bones (Figs. 60, 65). There also seems to be an ethmoid commissure through the lateral rostrals and rostral, and there are ample pores to suggest that there were parasagittal connecting commissures as well (Figs. 60, 65).

Three accessory elements lateral to the most anterior three lateral supraorbitals are emarginated both dorsally and ventrally for pores. Ventral to these elements and posterior to the rostral are a thin anterolateral and posterolateral rostral, each with very large pores. The posterolateral rostral also bears the descending nasal prong, against which the posterior end of the premaxilla abuts. The antorbital forms the anterior border of the orbit and bears two to three large pores, but it cannot be determined whether these pores are associated with the posterior pores of a rostral organ as in *Latimeria* (Millot and Anthony, 1958) or with an antorbital branch of the infraorbital lateral line canal (posterior lateral commissure, Fig. 74). All bones of the ethmosphenoid moiety are tightly abutted against one another.

Cheek.—The lacrimojugal and cheek bones are all thin, and lateral line canals and pores are difficult to trace. All bones are vertically oriented and, except for the postorbital, deeply overlapping (Fig. 60). The anterior margin of the postorbital is level with the intracranial joint. The preoperculum overlaps the posterior end of the lower jaw.

The operculum has a well developed articular facet that fits in a condyle near the posterolateral corner of the tabular. It cannot be determined whether this might represent the fusion of hyomandibular and opercular elements. The suboperculum is thin but prominent.

Oticooccipital.—The anterior end of the otic canal
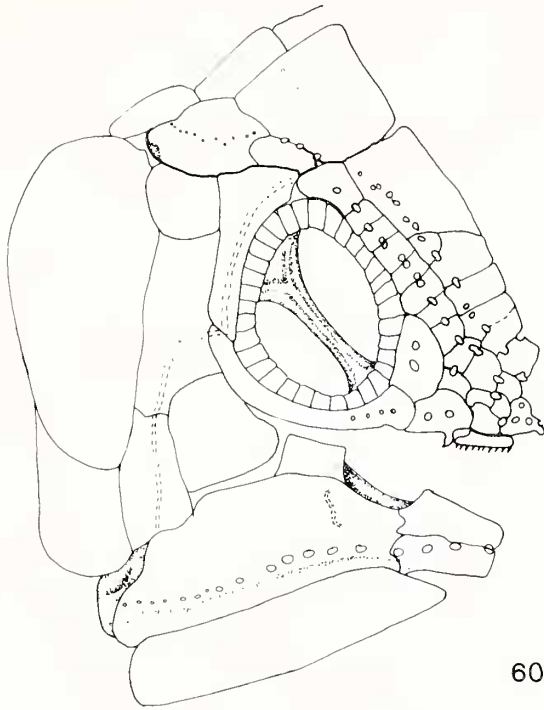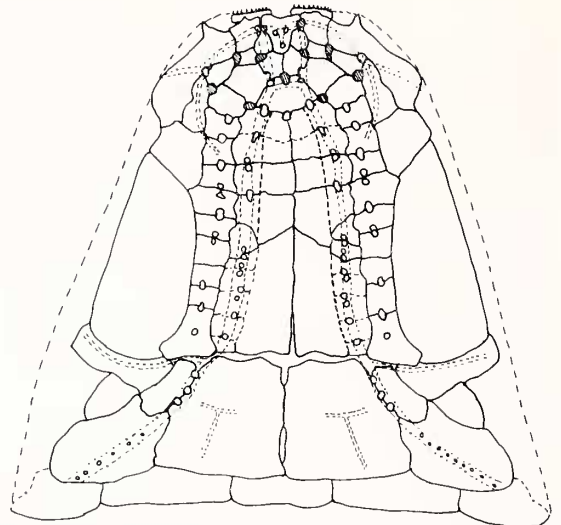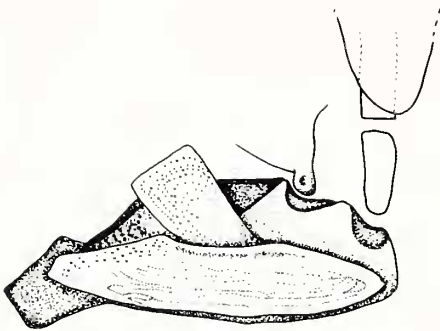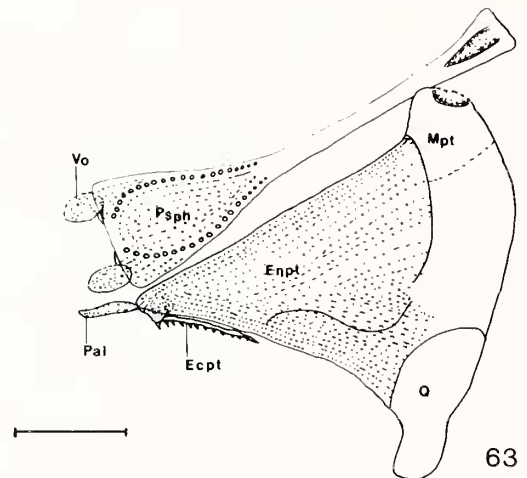
Fig. 60.—*Allenypterus montanus,* restoration of the bones of the lateral surface of the head, based on MV 3091, 5381.
Fig. 61.—*Allenypterus montanus,* restoration of the bones of the head in dorsal view, based on CM 27286, 27287, 37509.
Fig. 62.—*Allenypterus montanus,* internal view of lower jaw, based on MV 2949, CM 27287 and 37509.
Fig. 63.—*Allenypterus montanus,* palate and parasphenoid of CM 27286. See Fig. 64.

is beneath the supratemporal-postparietal suture, and gives off several large pores between the two bones (Figs. 61, 64). The tabular is greatly extended posterolaterally; much of the tabular, however, is unornamented. The posterior wall of the dorsal end of the spiracular canal is formed by the tabular with a contribution from the supratemporal. Pit lines in the postparietals are variable but often T-shaped, the posterior pit line extending to the rear margin of the postparietal. Contralateral postparietals are never sutured together in smaller individuals (Fig. 64) and rarely firmly joined even in the largest specimens.

There are 5 bones in the extrascapular series. Canals cannot be definitely traced in these bones. The posttemporal, if present, was small and thin.

Palate, lower jaws, and branchials.—The palate of *A. montanus* is relatively short and quite high in

Fig. 64.—*Allenypterus montanus,* CM 27286, lateral view of head. Arrow points to median ventral scale shield. Scale in mm.

Fig. 65.—*Allenypterus montanus,* CM 37509a, anterior part of head. Arrows indicate dorsal midline. Scale in mm.

Fig. 66.—*Allenypterus montanus,* CM 37509b, anterior part of head. Scale in mm.

proportion to the head. The location of the external projection of the quadrate-articular joint at the level of the rear of the orbit in those specimens preserved with depressed heads is farther forward than in any other coelacanth except "*Diplurus*" *newarki* (Schaeffer, 1952). The palate bears relatively straight lines of fine denticulations divergent from the anterior end of the endopterygoid. The autopalatine is rarely

seen and may have been weakly ossified; dermopalatines are thin and bear very fine teeth. The palate lacks any trace of a notch or facet for the reception of a basipterygoid process or basal articulation with the braincase.

The anterior end of the lower jaw, consisting of dentary occlusally and splenial below, describes an obtuse angle with the long axis of the angular. The dorsal edge of the angular shows a diastema, or concavity between the posterior end of the dentary and the coronoid. The mandibular canal exits through large pores in the splenial and anterior part of the angular, and continues rearward through finer pores, to pass from visibility at the posterior end of the angular. The pores of the canal do not curve upward posterior to the jaw articulation. The rear margin of the lateral surface of the lower jaw is separately ornamented and may represent coossification of a dermal element with the underlying retroarticular region of the articular (Fig. 60). In mesial view, fine teeth on one or more very thin plates line the dentary, and a thin precoronoid is continuous between the posterior end of the dentary and the prominent coronoid (Fig. 62). The posteroventral end of the coronoid lies mesial to the anterior end of the articular ossification, that in turn is apparently only coossified with the angular ventral and lateral to the articular facet. Several specimens, such as CM 27287, suggest that the retroarticular and articular regions of Meckel's cartilage ossify separately and fuse relatively late in development. The symplectic facet is located posterior and ventral to the articular facet. The prearticular spans the entire lower jaw from below the symplectic facet to the ventromesial bend in the dentary-splenial. The symplectic and epihyal are visible in MV 2949, the ventral end of the epihyal coinciding with the ventral edge of the operculum, the symplectic underlying the suboperculum.

The operculum bears an anterodorsal process extended from a slight ridge on its mesial surface that articulates with the posterolateral edge of the tabular. As this would coincide with the position and articulation of the hyomandibular with the braincase, we suggest that the hyomandibular has fused to the operculum.

The branchial arches do not appear to differ significantly from those of other coelacanths, apparently lacking pharyngobranchial elements. The arches all bear long, delicate gill rakers, however.

Shoulder girdle.—The anocleithrum has a slight but clear anterodorsal bend that renders it S-shaped in lateral view; it lacks evident contact with the head

(Fig. 57). The cleithrum is quite elongate, with an ornament of long, thin vertical lines. The anteroventral process of the cleithrum and the posterodorsal, or cleithral process of the clavicle are thin and elongate, both overlapped by the extensive extracleithrum (Fig. 59). The clavicles are thickened and posteriorly expanded in the ventral midline, and do not suture across the midline. The thickened, deep and highly overlapping median ventral scale row, extending from the posterior ends of the clavicles to the middle of the pelvic plates, remains attached to these elements even after severe postmortem disruption of the abdominal cavity (Fig. 64). It must be presumed that there were strong ligamentous attachments among these elements.

Postcranial skeleton.—An ossified swim bladder is present.

The first six neural arches are wide, stout and closely fitted, with short neural spines only upon the last three. The remainder of the axial elements are as in other coelacanths (Fig. 57). The first dorsal fin plate is rounded, showing no trace of fusion from supraneural elements. The second dorsal fin plate is simple, rounded, and its shaft is intercalated between two neural spines, usually the 11th and 12th abdominal neurals. The epichordal lobe of the caudal fin begins one or two segments behind the end of the second dorsal fin, 8 segments in advance of the first caudal vertebral element.

The pelvic plates are large, high, very thin triangular elements intimately associated with the posterior end of the median ventral scale shield. They seem to lack significant perichondral ossification. The pelvic fins are placed at the rear of the abdominal cavity, immediately in advance of the anal fin, and the anus is located between the pelvic fins. There seems to be no visible possibility of extension of the gut behind the anus. Gut infillings have been found; these consist of amorphous calcium phosphate and never contain recognizable material on gross examination.

The anal fin plate is supported below the first haemal spine, against the anterior face of the second haemal, and is anteroposteriorly elongated. Separate infrahaemal elements begin at the sixth haemal spine; there may be up to 45 infrahaemals. The fin rays of the ventral caudal lobe are miniscule, not articulated, and occur in 2:1 ratio with their endoskeletal supports from about the 36th haemal spine. They grade into an even finer series of rays posterior to the end of the caudal endoskeleton, on the vermiform extension of the body axis (Fig. 59).

The last three trunk segments and the first sixteen caudal segments of MV 5381 seem to show very thin, faint ossification of the vertebral centra consisting of fused dorsal and ventral elements. Details, however, cannot be resolved and cannot be confirmed on any other specimen.

Discussion.—The unique body form of *Allenypterus montanus* and the ecomorphological relationships of the remainder of the Bear Gulch coelacanths have been discussed elsewhere (Lund et al., in press) and need not be elaborated upon here. In summary, however, *A. montanus* is well adapted to a shelter dwelling life and extremely slow undulatory motion through the use of the long low epichordal caudal fin. High maneuverability is inherent in the use of the high, compressed body with the size and distribution of the paired and median fins around the center of buoyancy in the short trunk. The total lack of surface area at the caudal extremity, an aspect ratio effectively of zero, indicates that rapid acceleration for escape from predation could be provided only by a quick stroke of the caudal region of the body and would be of low effectiveness. *Allenypterus* would be very unlikely to survive outside the shelter of algal or sponge thickets. The small ventroterminal mouth, restricted gape, tiny teeth and long gill rakers indieate a feeder upon rather small and relatively soft bodied organisms.

The uniquely adapted body form of *A. montanus* does not, at this time, constitute sufficient reason to place it in its own, and necessarily monotypic, family. It shares an equal number of unique and probably derived characters with *Hadronector* and *Polyosteorhynchus*. It also shares the high ratio of fin rays to endoskeletal supports with *Lochmocercus, Diplocercides,* and *Coelacanthopsis curta*: a primitive character of little systematic or phylogenetic utility.

Suborder *Incertae sedis*

Genus *Lochmocercus* Lund and Lund, 1984

Type species.—*Lochmocercus aciculodontus* Lund and Lund, 1984.

Provisional diagnosis.—Coelacanths with relatively long trunks. Moderate size supratemporal bone bears pores for anterior end of otic canal; antorbital with two pores, lacrimojugal with pores, and complete cheek tightly fit together. Anterior margin of postorbital close to intracranial joint. Lower jaw lacks anterior angular diastema and margin continuous from dentary through precoronoid to anterior

margin of coronoid. Dentary and precoronoid bear a row of large teeth. Opercular flap with both operculum and suboperculum. Anocleithrum stout and may have contacted rear of skull, cleithrum short with a long anteroventral process, clavicles short and extracleithrum tightly sutured to cleithrum. First dorsal fin plate shows ventral digitiform processes, second dorsal plate simple, rounded above and articulates dorsally with presumed fin axis. Pelvic plate quadrangular and lacking in significant perichondral bone: its axial elements are ossified. Fin rays of caudal fin in 2:1 ratio to endoskeletal supports.

Discussion.—The genus *Lochmocercus* resembles members of the Hadronectoroidei in characters of bones of the cheek, oticooccipital moiety, lower jaw, and the supports for the dorsal and pelvic fins, and in doing so is conspicuously divergent from *Diplocercides.* There is insufficient information on critical characters in the ethmosphenoid moiety, due to a lack of well preserved specimens, to definitively assign this genus to either suprageneric group. One other coelacanth taxon besides *Diplocercides* and *Allenypterus* has a 2:1 ratio of caudal fin rays to endoskeletal supports, *Coelacanthopsis curta* Traquair (1905). The type and only specimen of *C. curta* has had the midsection of the body faulted under the caudal region, and has no distinguishable cranial elements, so comparisons are difficult. The shoulder girdle of *C. curta,* however, is indistinguishable in proportions or ornamentaation from that of *Lochmocercus.* It is felt that future specien of *C. curta,* were they to be found, would indeed be recognizable and that the name cannot be buried or obliterated.

Lochmocercus aciculodontus Lund and Lund, 1984
Figs. 67–70

Previous reference.—"Bushy tail," Lund et al., in press, Fig. 1.—*Lochmocercus aciculodontus* Lund and Lund, 1984.

Type specimen.—MV 6218.

Referred specimens.—CM 27406, 30715, 35201.

Horizon and locality.—Namurian A (E2B), Lower Carboniferous Bear Gulch Limestone member of the Heath Formation, Big Snowy Group, south of Becket, Fergus County, Montana.

Provisional diagnosis.—Trunk long relative to height, size to over 92 mm standard length. Bones of skull roof sparsely ornamented with coarse tubercles, other external head bones more densely ornamented. There are 31–33 neural spines in trunk, 4+23–28 fin rays in both dorsal and ventral aspects

Table 5.—*Proportional statistics of* Lochmocercus aciculodontus. *Abbreviations as in Table 1.*

Statistics	$\dfrac{\text{Max. ht.}}{\text{SL}}$	$\dfrac{\text{HL}}{\text{SL}}$	$\dfrac{\text{GL}}{\text{HL}}$	$\dfrac{\text{GL}}{\text{SL}}$	$\dfrac{\text{GL}}{\text{LJL}}$	Asp. R.
N	1	3	2	2	2	1
Mean	.4487	.2427	.444	.1048	.5336	.9524
SD	—	.0219	.0058	.013	.005	
Var.	—	.0003	.00001	.00008	.00001	

of caudal fin, rays of first dorsal fin are 3+8, of second dorsal fin are 2+9. Caudal outline is elliptical. Proportional characters given in Table 5.

Description.—*L. aciculodontus* is the rarest and the most poorly preserved of the Bear Gulch coelacanths. The rostral region is not completely preserved on any single specimen, nor is there any complete axial skeleton attached to a head. The parasphenoid of the holotype, MV 6044, can be seen posteroventral to the anal fin in Fig. 67. Thus there are few reliable details of the ethmosphenoid moiety available at present. Further, there is no convincing evidence that the largest available specimen represents a mature individual. Nevertheless, many salient details of the osteology are available.

The only available ethmosphenoid moiety of the skull roof has been disrupted (Figs. 67, 68). Large parietals, laeking any trace of a lateral line canal form the supraorbital region, and there are indications of at least two pairs of frontonasals anteriorly. Laterally, a single series of supraorbital bones is visible, approximately six of which roofed the orbital rim. The antorbital is large, and bears two pores as if for the rostral organ, and anteriorly the pos-

terolateral rostral bears few, large pores for the infraorbital lateral line canal and an anteroventral nasal prong. A dislocated element immediately anterior to the posterolateral rostral is probably an anterolateral rostral; it is perforated or bordered by at least one pore. The premaxilla is seen as a low strip of bone bearing a few long, sharp teeth.

The lacrimojugal is unusual in showing a long series of prominent, although small, infraorbital canal pores. The infraorbital canal passes from the middorsal margin of the heavy postorbital to the skull roof at the anterior end of the supratemporal. The prespiracular is large, thin and rounded, forming the spiracular operculum. The jugal lateral line canal turns ventrad to enter the anterior margin of the preoperculum. A quadratojugal pit line cannot be resolved.

The opercular series contains a long, ventrally tapering operculum and a tall, narrow suboperculum.

The dermal bones of the oticooccipital moiety of the skull consist of large postparietals bordered posterolaterally by the supratemporals and tabulars. The supratemporal does not extend forward to the in-
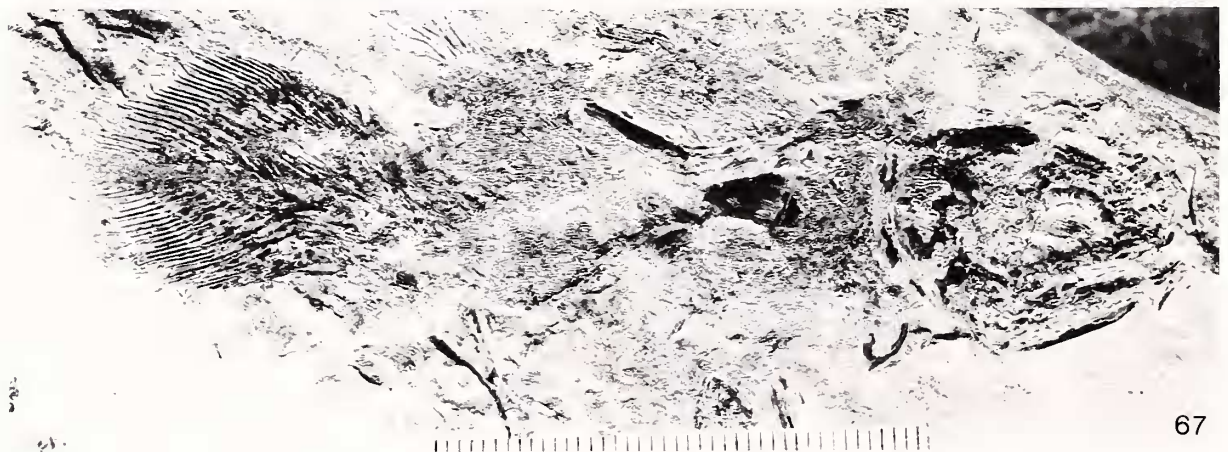

67

Fig. 67.—*Lochmocercus aciculodontus,* type, MV 6044. Scale in mm.
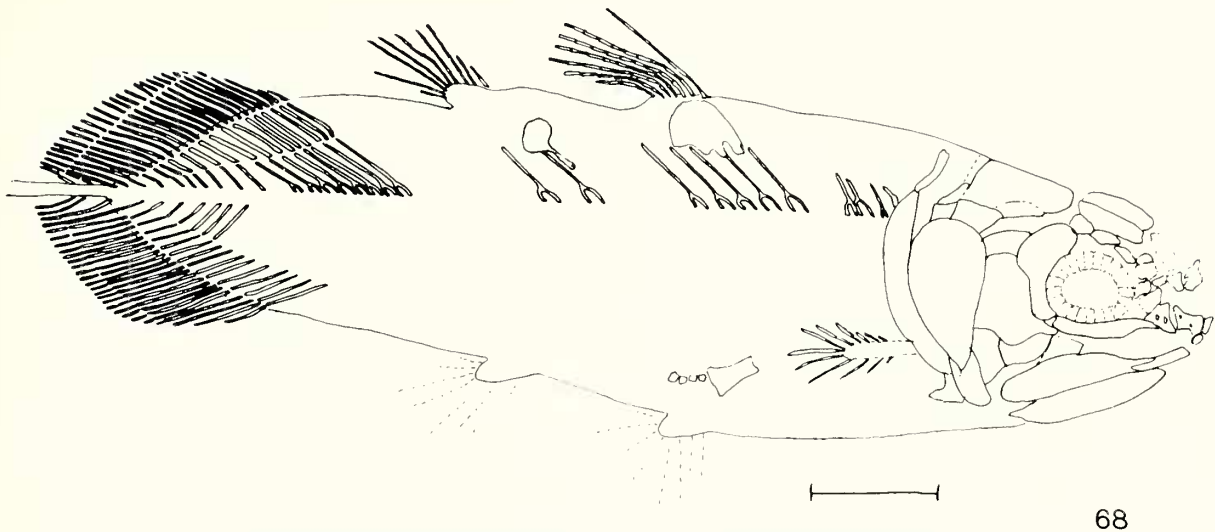
Fig. 68.—*Lochmocercus aciculodontus,* restoration based on MV 6044.

tracranial joint. A branch of the supraorbital lateral line canal enters the anterolateral margin of the post-parietal anterior to the supratemporal and ends in a large pore at the level of the middle of the supra-temporal. The transverse supraorbital commissure apparently joins the infraorbital eanal to form the otic canal, which appears to continue through the supratemporal into the tabular. Several large pores are visible in the tabular. Ornamentation is sparse on the oticooccipital moiety.

There are five very thin bones in the transverse occipital commissure.

The autopalatine ossification is stout and trian-gular, articulating with the ethmoid region lateral to large, heavily toothed prevomers (Fig. 70). The ec-topterygoid extends to the level of the coronoid on the lower jaw. The endopterygoid bears few, rela-tively coarse ridges paralleling its dorsal margin. The metapterygoid is stout, and articulates with the relatively short antotic process. The quadrate pro-jects significantly posterior to the level of the antotic process. There is no visible indication on the palate of articulation with any process of the braincase.

The oral margin of the dentary bears large, long sharp teeth, and is continuous posteriorly with the dorsal edge of a precoronoid that also bears a row of teeth (Fig. 70). The oral margin of these two bones extends uniformly posteriad to the base of the cor-onoid. While there is no angular diastema, the oral margin of the dentary and the precoronoid are me-sially inset in relation to the lateral laminae of the

dentary and the angular. The splenial bears a few large pores anteriorly, with relatively small pores of the mandibular lateral line continuing through the angular. The articular element is as strongly ossified along its anterior surface as along the posteroventral surface of its quadrate condylar fossa. The retroar-ticular area of Meckel's cartilage seems to be sep-arately ossified (Fig. 70).

Branchial arches are not well known.

The shoulder girdle is most noteworthy for being a very tightly integrated structure, lacking the rel-atively loose and flexible association of clavicle, ex-tracleithrum and cleithrum seen in most other coel-acanths. There does seem to be an extracleithrum, and a large one, but it is tightly held to the associated bones and lines of ornamentation are continuous across the cleithrum-extracleithrum boundary. There is ossification in the scapulocoracoid cartilage, but details cannot be resolved.

Discussion.—There is scarcely adequate infor-mation about the osteology of *L. aciculodontus* upon which to judge its relationships. There are several noteworthy primitive characters, such as the rela-tionships of the bones of the lower jaw, that differ-entiate it most strongly from *Hadronector* and *Al-lenypterus*; the caudal fin ray ratio, that differentiates it from *Hadronector* and *Polyosteorhynchus*; and the stout anocleithrum, tight association of cleithrum and clavicle, and the passage of the supraorbital canal into the postparietal, that separate it from all Hadronectoroidei. The apparent single supraorbital
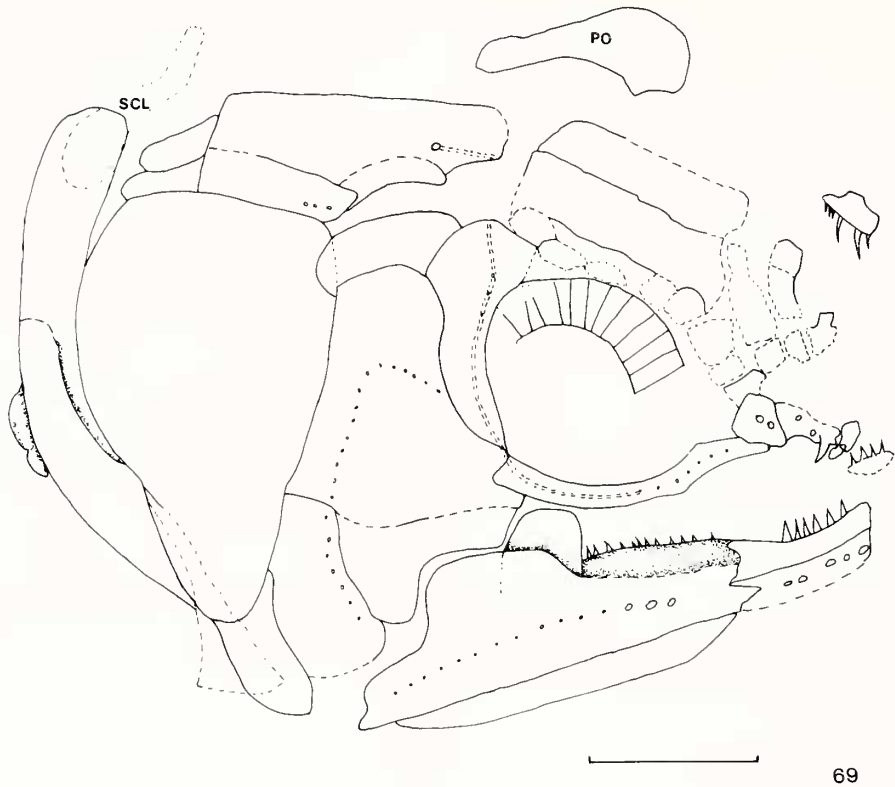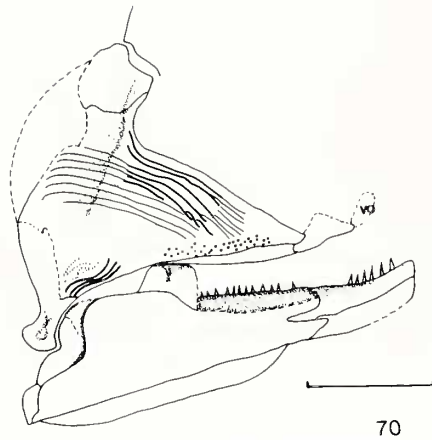
Fig. 69.—*Lochmocercus aciculodontus*, reconstruction of the head of MV 6044.
Fig. 70.—*Lochmocercus aciculodontus*, palate and lower jaw of MV 6044.

series contrasts strongly with the complexities of *Polyosteorhynchus, Allenypterus* and *Hadronector*. The supratemporal is reduced by comparison with the three Hadronectoroidei, but large in comparison with Coelacanthoidei. Ornamentation of the skull roof is sparse, but this could signify nothing more than rather immature individuals.

Lochmocercus shares a suite of primitive char-

acters with Hadronectoroidei but with no member of the Coelacanthoidei. These include the five bones in the tightly knit cheek, the supratemporal, the suboperculum, and the apparent lack of a basipterygoid process. It shares with *Allenypterus* as well as the coelacanthoid *Diplocercides* only one common character, the primitively high caudal fin ray : endoskeletal support ratio.

DISCUSSION

GROWTH, DEVELOPMENT, AND SPECIES IDENTIFICATION

Several characteristics have, in the past, been suggested or used in attempts to identify and diagnose species of coelacanths (Schaeffer, 1952; Moy-Thomas, 1937; Forey, 1981). Scale ornamentation, for instance has been used to diagnose the "genus" *Chagrinia* (Schaeffer, 1962), and to place various fish into the "species" *Rhabdoderma elegans* without cranial osteological knowledge. Virtually nothing has been said about scale ornamentation in the descriptive portion of this paper, for several reasons. The first is simply that scales of *Caridosuctor* have an ornament of few, tightly packed lines slightly convergent at the posterior midline of the scale, but that the variation accounted for by position on the body and by specimen size prevents further analysis. Scales are not present on the 30 mm *Caridosuctor* and unornamented on the 42 mm specimen. Growth characteristics of the other species are more complex. Scales of *Hadronector, Allenypterus,* and *Polyosteorhynchus* specimens, when large, are all similarly ornamented with few, straight, relatively thick lines and are indistinguishable. The scales of *Lochmocercus* are tuberculated in the one specimen with scales. However, *Allenypterus* up to the 44 mm specimen are faint and indistinguishable, and specimens of larger sizes rarely preserve with distinct scales, until over 100 mm in length. It is not known at what length *Polyosteorhynchus* develops scales, as neither of the very well preserved 35 mm specimens has scales and the poorly preserved intermediate sized specimen does not show scales. The condition for small *Hadronector* is unknown. Although there are two small specimens of *Lochmocercus,* both lacking scales, this may have been a preservational factor. It has proved futile to use scales for identification within the Bear Gulch coelacanths.

Ornamentation, particularly of the gular or opercular, has been traditionally used to erect species in the British Carboniferous. This matter has been explored in regard to the *R. elegans-R. lepturus* question, above, but should be amplified upon. All species of coelacanths in the Bear Gulch are born without external ornamentation of any kind. Generally, only the fin rays, axial skeleton, shoulder girdle, lower jaws, and branchial arches are evident in the smallest specimens of all species. Among the members of the Hadronectoroidei, in *Allenypterus* and *Polyosteorhynchus* the smallest individuals are between 28 and 35 mm long, but individuals at around 70–80 mm display the first signs of virtually identical ornamentation (Fig. 52). The ornamentation of the 92 mm *Lochmocercus aciculodontus* is coarse and sparse, characteristic of *Allenypterus* and at about the same size. Specimens of *P. simplex* over 100 mm have an opercular and cheek ornamentation clearly distinguishable from that of any other coelacanth in the Bear Gulch (Figs. 49, 51), but variation in the osteology of the cheek is significant. Large *Hadronector* may be distinguishable from other coelacanths in the Bear Gulch fauna on the basis of the combined ornamentation and bone thickness, simply because no other has thick cheek bones. Finally, ornamentation of *Caridosuctor* on the gulars and operculum is usually recognizable, but these elements are primarily recognizable on the basis of size and proportions, the articulation with the tabular, and full knowledge of the tremendous variability in ornamental pattern. Even the bones of the cheek of *C. populosum* may be ornamented or unornamented at any given size up to that of the largest individuals. The use of ornamentation, without correlating it with size and proportions over a large range of sizes, is what led Newberry (1856) to name three species of *Rhabdoderma* from Linton, Ohio, only to later question his own taxa (Newberry, 1873). The use of ornamentation to diagnose species, at the level of detail discrimination that characterizes paleontologic practice, is an exercise in futility.

Vertebral counts have proved useful in the Bear Gulch coelacanths only with great caution. The ability to discriminate regions of the column makes it possible to avoid the uncertainties of covered anterior neurals. Counts of caudal segments are highly uncertain in light of the progressive ossification of the most posterior neural and haemal spines. Suites of specimens within a fauna can be distinguished with the help of vertebral counts, but not solely by use of this character.

Growth characteristics and proportions of the Bear Gulch coelacanths are all extremely similar in pattern and diverge from a common set of body proportions in simple linear fashion separated by very fine, highly significant statistical differences (Table 6, Figs. 71, 72). Corresponding details of osteology show similar proportional differences. Among the most significant are those that can be related to functional separation of the species, such as gape length and aspect ratio (Table 6; Lund et al., in press), and the shape of the caudal fin. In this regard, however, it should be noted that the shape of the caudal fin

Table 6.—*Relationships among Bear Gulch coelacanth species and body ratiois.*

Statistics	Large				Small
Mx. ht. / SL	*A.m.*	*H.d.*	*P.s.*	*C.p.*	
	.3598	.3508	.3314	.2256	
HL / SL	*P.S.*	*H.d.*	*A.m.*	*C.p.*	
	.2288	.2062	.1874	.1596	
GL / HL	*C.p.*	*H.d.*	*L.a.*	*P.S.*	*A.m.*
	.4833	.4708	.444	.3895	.3598
GL / SL	*L.a.*	*H.d.*	*P.S.*	*C.p.*	*A.m.*
	.1048	.0957	.0934	.0796	.0666
GL / LJL	*L.a.*	*H.d.*	*P.S.*	*C.p.*	*A.m.*
	.5336	.5187	.5067	.4891	.4567
LJL / SL	*H.d.*	*P.S.*	*C.p.*	*A.m.*	
	.1869	.1801	.1584	.1434	
Asp. R.	*H.d.*	*P.S.*	*L.a.*	*C.p.*	*A.m.*
	1.188	1.133	.9524	.7989	

of *Polyosteorhynchus* changes from elliptical to square cut over its recorded size range. There are insufficient data to determine whether this is a gradual change or one that occurs in the transition from larval to adult conditions, as has been documented for many Bear Gulch actinopterygians (Lowney, 1980). It is also worth noting that while high growth rates of height parameters around the oticoccipital moiety of the head and the trunk of *Allenypterus* relative to long measures account for the greatest part of its unusual adult shape (Fig. 58), ratios of longitudinal parameters fit with the same degree of fine spacing as seen in the other coelacanths of the fauna (Figs. 71, 72, Table 6). These differences apply within the Bear Gulch fauna, but their utility in distinguishing species among faunas would appear to be very limited, given the possibility of character displacements with different interspecific interactions than the ones found herein.

Attempts were made to analyze distance from the snout to the origins of dorsal fins one and two as in Schaeffer (1952), but it was found that intraspecific variation rendered this character meaningless in the Bear Gulch fauna and extremely suspect in the original application. There is no indication in specimens of *Rhabdoderma elegans* or of any Bear Gulch coelacanth of the extraordinarily long median lobe of the caudal fin that Schultze (1972) found in *R. exiguum* fetuses. There is a decrease in the median lobe : standard length ratio of *Caridosuctor* from .0785 at 79 mm to .0684 (N = 6) in the 120–140 mm range, to .0648 (N = 3) at the 179–182 mm range, to .0540 in the 200–220 mm range (N = 2). A similar decrease can be seen in *P. simplex*.

Nothing can be said about the growth of *Hadronector donbairdi* because specimens have only been reliably identified between 91–108 mm in standard length. This may be an artifact of sampling in view of the relative scarcity of the species, although assorted sizes are known for all other coelacanths. Of the remaining coelacanths, there is a striking disparity between the standard lengths of the two smallest, *C. populosum* 30 and 42 mm, and the majority of the specimens, starting at 79 mm (Fig. 72). The smallest *Caridosuctor* are considerably smaller than *Rhabdoderma,* which clearly had large yolked eggs. Among other known Rhabdodermatidae, the size range of yolk sac bearing individuals of *Rhabdoderma exiguum* is around 49–55 mm (Schultze, 1972, 1979), and the minimum known size of *R. elegans* is around 49 mm.

The reproductive mode of *Latimeria* involves probable internal fertilization (Griffith and Thomson, 1973), large yolked eggs, and fetuses that are retained in the oviduct of the mother without further maternal nutritional contribution and without a hard protective shell (Smith et al., 1975). The size of the unprotected eggs and fetuses of *Latimeria* virtually demands a strategy of perinatal care, as must the fetuses of *Rhabdoderma* and possibly *Caridosuctor.* Migration to a protected spawning ground could constitute such strategy.

There are morphological features found in the coelacanths with known relatively larger eggs that may be at least in part associated with prolonged retention of fetuses to larger absolute size at birth. These include the broad, medially articulated pelvic girdles, the shift to midabdominal location of the pelvics (see *Allenypterus* for the opposing condition), and the posterior extension of the peritoneal cavity. It must be pointed out that these features are shared by *Hadronector* and the Coelacanthoidei.

Retention of the fetus to an advanced size and migratory spawning are not correlated adaptations, but both constitute significant adaptations for perinatal care among vertebrates (Lund, 1980; Wourms, 1977). It is suggested that advanced retention of young represented the most significant adaptive advance of the Coelacanthoidei. The varying reproductive strategies of the "guild" of coelacanths in
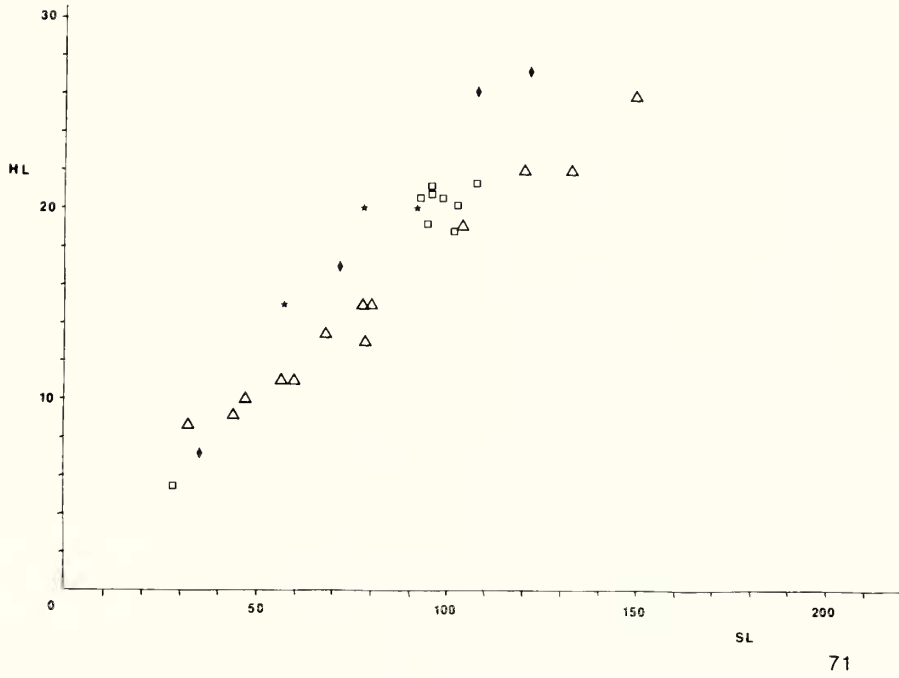
71
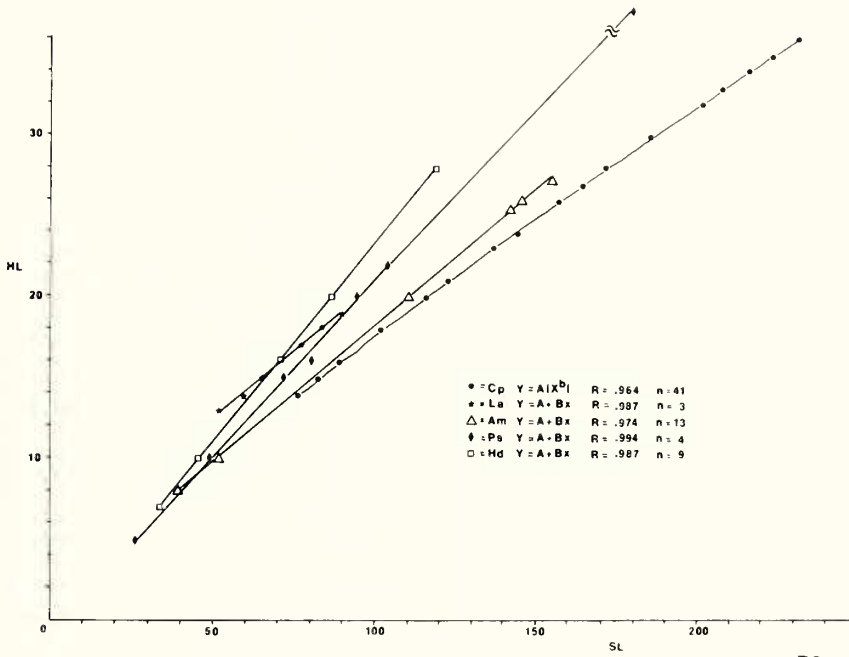
72

Fig. 71.—Graphs of head length to standard length for *Allenypterus montanus* (triangles); *Hadronector donbairdi* (squares); *Lochmocercus aciculodontus* (stars); and *Polyosteorhynchus simplex* (diamonds).

Fig. 72.—Graph of regressions of head length to standard length for *Caridosuctor populosum* (Cp), *Lochmocercus aciculodontus* (La), *Allenypterus montanus* (Am), *Polyosteorhynchus simplex* (Ps), and *Hadronector donbairdi* (Hd).

the Bear Gulch fauna, however, are also significant. The coexistence of five species of coelacanths in the same, rather small basin could in part have been aided by resource partitioning based upon fine differences in feeding and swimming mechanisms (Table 6; Lund et al., in press; Schoener, 1974; Gatz, 1979). There is, however, very little overlap in potential resource utilization between groups of young fish differing as radically in size at first appearance as *Caridosuctor, Hadronector,* and the remainder of the Bear Gulch coelacanths.

Lateral Line Homologies

The lateral line canals, or more properly the neuromast organs, are vital landmarks in the determination of bone homologies among Placodermi (Ørvig, 1975; Miles, 1977) and Osteichthyes (Jarvik, 1948; Jollie, 1980; Westoll, 1949; Denison, 1968; Lowney, in press), and have a critical, if unclear, relationship to the process of induction of the dermal skeleton through the formation of sensory placodes from neural crest ectomesenchyme. The inductive process, while it need not be the concern of this article, is currently thought to work in a manner similar to that now known in the induction of ameloblast and dental papilla during odontogenesis (Kollar, 1978). Even in the Chondrichthyes and Acanthodii, where the formation of the dermal bones of the head is either absent or apparently unrelated to the lateral line canals, scales immediately adjoining the canals are modified in some manner (Miles, 1973; Zidek, 1976; Patterson, 1965), indicating that there is some inductive relationship. That this relationship is not a simple one is clear from studies of ontogenetic variation in many fish (Jarvik, 1948; Parrington, 1949; Jollie, 1980; Pehrson, 1947, for examples) including *H. donbairdi* and *A. montanus.*

The lateral line sensory canals of the heads of the gnathostome fishes display a series of variations upon a conservative pattern, many elements of which can be readily homologizable among the classes. The pattern consists of a limited number of longitudinal canals variably joined by segmentally arranged transverse canals (Ørvig, 1975; Jarvik, 1948; Stensiö, 1947; Westoll, 1949; Pehrson, 1947; Jollie, 1980; Lowney, in press). This pattern in turn corresponds sufficiently with the canal pattern seen in the carapace of various heterostracans (Säve-Söderbergh, 1941; Ørvig, 1975; Lowney, in press) that it can be accepted as a model for the primitive condition of the sensory canal system of the gnathostomes.

Complicating the study of the lateral line canal system and related bones among the Osteichthyes is that paleontological evidence has been so incomplete that little useful information could be added toward determination of the applicability of details of the model to evolutionary patterns within the class. The coelacanths have not previously provided sufficient information to document certain gross homologies, whereas the previously available actinopterygian evidence, particularly from the Paleozoic, has been very limited (Stensiö, 1947). Lateral line canal information from the Bear Gulch Osteichthyes has added considerable information.

In spite of considerable variation among taxonomic groups, the homologies and the basic names of the longitudinal canals and several of the transverse canals seem to be agreed upon (Fig. 73). Thus the longitudinal canals are the supraorbital, the otic (epibranchial), infraorbital (including jugal, perhaps including supramaxillary) and the mandibular. These canals are variously joined by cross commissures. The rostral region is very rarely preserved and yields the least comparative information but may have two commissures across the dorsal midline, the ethmoid anteriorly and the antorbital behind it. Two lateral commissures are indicated between the supraorbital and infraorbital canals antorbitally, the anterior lateral and posterior lateral commissures. Posteriorly, the supraorbital and otic canals may be joined by at least two major lateral commissures, the transverse supraorbital and the transverse otic. An anterodorsal branch of the postorbital, the supraorbital branch of Miles (1977) has been suggested as a branch of a separate longitudinal epibranchial canal by Poplin (1973) and supported by Thomson and Campbell (1971). Evidence for this branch can also be found in part in heterostracans (Ørvig, 1975) and Actinopterygii (Lowney, in press) and suggests that it may be involved in links between the supraorbital and otic canals (Poplin, 1973). The otic canals are joined across the dorsal midline by the occipital (supratemporal) commissure, at or behind the rear margin of the braincase. The infraorbital canal may continue posterior to the orbit as the jugal canal, although the homologies here are far from agreed upon. It is connected to the otic canal dorsally by the postorbital canal and ends at the preopercular canal, which spans the side of the head from otic to mandibular canals. Additionally, there are reports of an opercular transverse canal (Lowney, 1980). Phylogenetic regression of lateral line canals may leave visible indicators in bones in the form of pit lines, or simply clusters or rows of naked neuro-
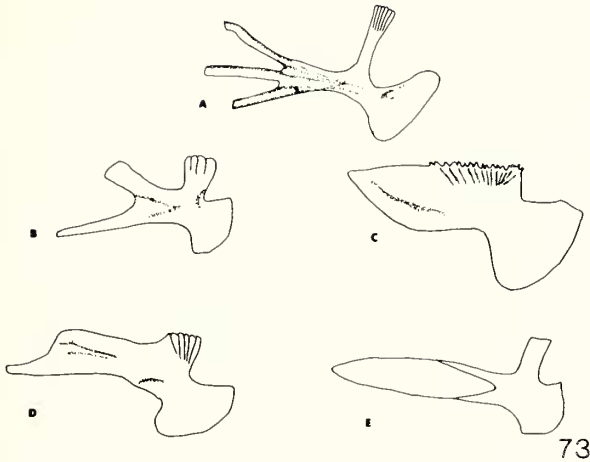
73

Fig. 73.—Pelvic plates of certain coelacanths. A) *Rhabdoderma elegans,* CM 23018; B) *Diplurus newarki* (after Schaeffer, 1952); C) *Wimania sinuosa* (after Stensiö, 1921); D) *Coelacanthus granulatus* (after Moy-Thomas and Westoll, 1935); E) *Undina* cf. *U. minuta* (after Schaeffer, 1941).

74

Fig. 74.—Idealized lateral line canal and pit line patterns of Osteichthyes. Abbreviations (sensory canals usually expressed as pit lines are in parentheses): (ap) anterior pit line; an, antorbital commissure; at, anterior transverse commissure; e, ethmoid commissure; ep, epibranchial branch; i, infraorbital canal; j, jugal (supramaxillary) canal; m, mandibular canal; O, opercular slit; oc, occipital (supratemporal) commissure; OR, orbit; Ot, otic canal; P, pineal (parietal) foramen; (PP) posterior pit line; pt, posterior transverse commissure; po, postorbital canal; pr, preopercular canal; (qp) quadratojugal pit line (oral canal); s, segmental trunk canals; ss, spiracular slit; su, supraorbital canal; (to) transverse otic commissure (transverse pit line) ts, transverse supraorbital commissure.

masts without traces upon the underlying bone (Freihofer, 1978; Stensiö, 1947); these sensory organs usually retain their normal innervations and relationships to the remainder of the lateral line system.

In some coelacanths of the Bear Gulch limestone, the supraorbital canal extends from a clear antorbital commissure to an intersection with the postorbital part of the infraorbital canal, receiving an apparent posterior transverse commissure anterior to the orbit. An ethmoid, anterior transverse and antorbital commissure can be demonstrated in *Allenypterus* (Fig. 61) and are strongly suggested for *Hadronector* and *Polyosteorhynchus* (Figs. 44, 55). Shortening of the snout seems to have been linked to the elimination of the antorbital commissure and posterior lateral commissure in Coelacanthoidei (*Caridosuctor,* Fig. 75C). Details of the intersection of supraorbital and postorbital canals are usually obscured by the intracranial joint, but in *Lochmocercus* the supraorbital canal continues into the postparietal to end at a pit and posterior pit line (Fig. 69). The junction of supraorbital and postorbital canals in this genus is clearly associated with another canal branch, possibly the transverse supraorbital commissure. Among other coelacanths, the postparietal contains an isolated series of pit lines, the anterior and posterior in *Polyosteorhynchus,* possibly a continuous pit line in *R. lepturus,* and posterior and transverse pit lines in *Hadronector* and *Allenypterus.*

In *Porolepis* and *Holoptychius* the supraorbital canal receives the postorbital canal directly, and continues posteriorly to end at the transverse and posterior pit lines (Fig. 76A, D). A transverse canal at the position of the transverse otic commissure carries the lateral line into the tabular and in essence to an extremely short otic canal. The canal pattern in the narrow roofed *Osteolepis* and *Eusthenopteron* is essentially as in later or more specialized coelacanths (Fig. 76B, E). Most Devonian dipnoans show a prominent anterior medial bend in the supraorbital canals, as do crossopterygians. Only *Chirodipterus* and *Dipterus valenciennesi* are indicated to have an antorbital commissure (Miles, 1977) at this point. Some Devonian dipnoans show complete or apparent connections through what may be a transverse supraorbital commissure with the supraorbital canal, such as *Dipterus valenciennesi* (Westoll, 1949; Fig. 76C), *Uranolophus* (Denison, 1968), and *Stomiahykus* (Bernacsek, 1977), whereas in *Dipno-*
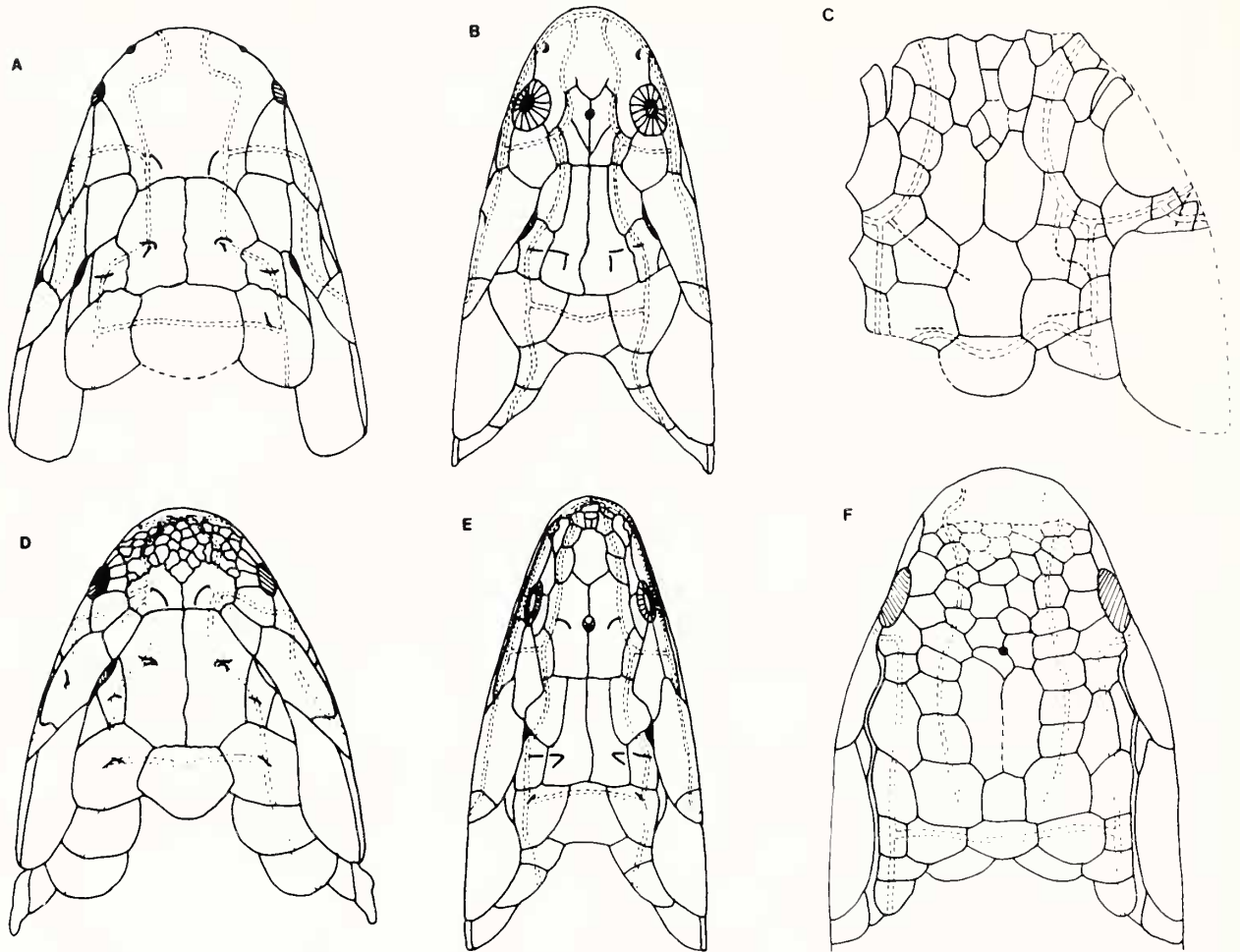
Fig. 75.—Coelacanth skulls. A) *Euporosteus eifeliensis,* ethnosphenoid (after Stensiö, 1937); B) *Allenypterus montanus*; C) *Caridosuctor populosum*; D) *Diplocercides kayseri* (after Stensiö, 1937); E) *Diplurus newarki* (after Schaeffer, 1952); F) *Macropoma mantelli* (after Watson, 1921).

rhynchus sussmilchi the supraorbital canal extends to the skull rear with no evident connection to the otic canal (Westoll, 1949, Fig. 76F). Many lungfish show regression of the supraorbital canal to pit lines posterior to the commissure, producing a pattern very similar to that of the later coelacanths, crossopterygians and many actinopterygians.

At the rostral region the apparent supraorbital canal meets the infraorbital canal anteriorly and crosses the midline at the ethmoid commissure in porolepids, osteolepids, and onychodontids (Jarvik, 1948; Andrews, 1973). The rostral regions of dipnoans are very poorly known and canals pass anteriorly and ventrally off the ossified rostral region in most. Miles (1977) maintains that there is no demonstrable ethmoid commissure in dipnoans.

Among Actinopterygii, an antorbital commissure between supraorbital canals is unknown. All known actinopterygians with the exception of one Bear Gulch taxon, "worm fin," (Lowney, in press; Lowney, 1980) lack an extension of the supraorbital canal anteromesial to the narial openings. In "worm fin" the supraorbital canal passes mesial to the nares anterior to a junction with a lateral commissure presumed be the anterior lateral. This commissure courses between the nares to join the infraorbital canal at the beginning of the ethmoid commissure. A short, blind canal extending dorsally from the infraorbital canal anterior to the rim of the orbit is believed to be a portion of the posterior lateral commissure. In *Acipenser* (Jarvik, 1948; Jollie, 1980), the supraorbital canal ends at the level of the narial
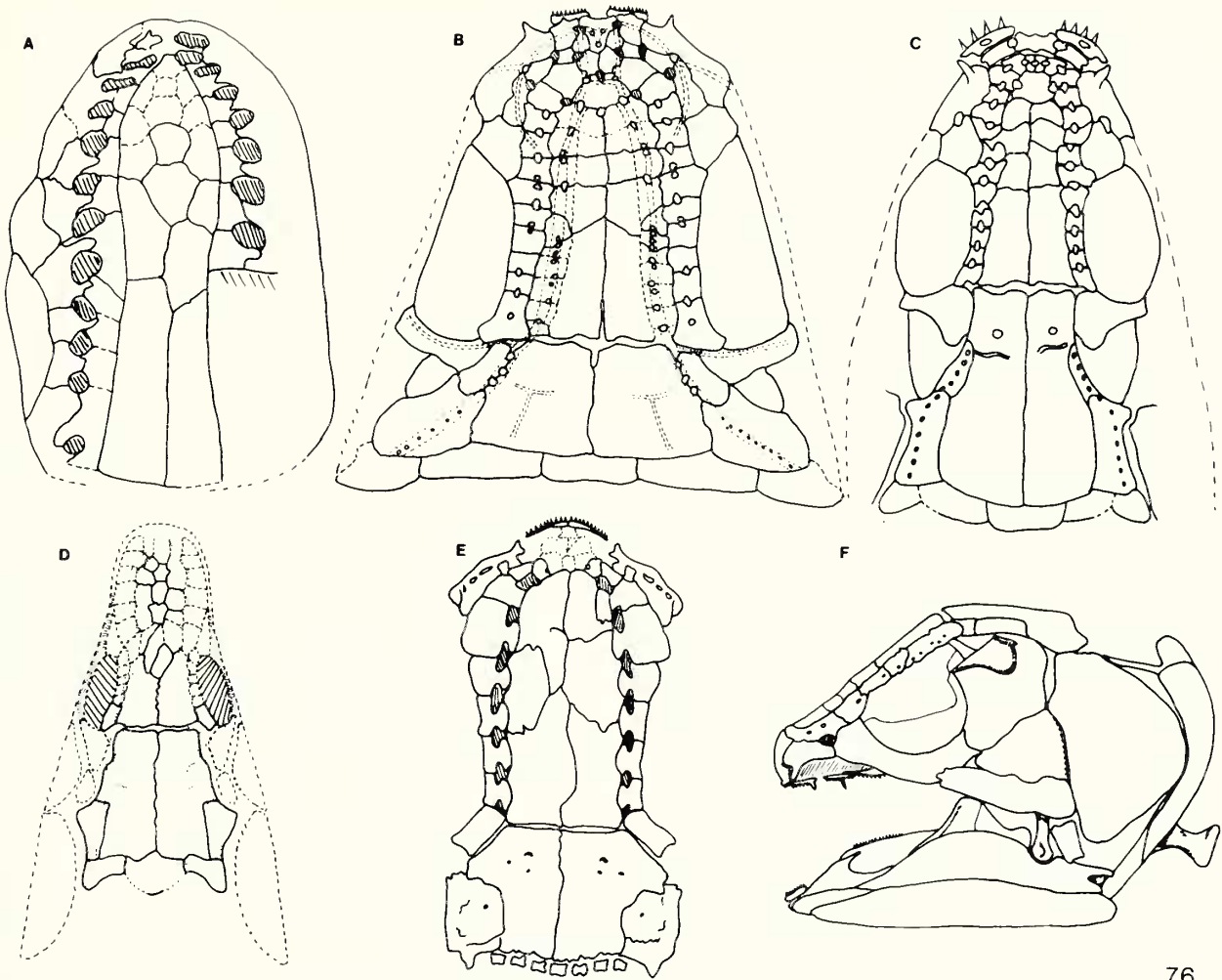
Fig. 76.—Sarcopterygian skulls. A) *Porolepis brevis*; B) *Osteolepis macrolepidotus*; C) *Dipterus valenciennesi*; D) *Holoptychius flemingi*; E) *Eusthenopteron foordi*; F) *Dipnorhynchus sussmilchii*. A, B, D, E, after Jarvik, 1972; C, F, after Westoll, 1949.

openings after giving off a ventrolateral branch that passes between the nares and ends blindly. The suprarostral row of nerve sacs has been interpreted (Jarvik, 1948:69) as a remnant of the anterior lateral commissure on the basis of its innervation. Among the teleosts, the canal between the narial openings (in the nasal bone) may communicate with the infraorbital canal anteriorly, near the ethmoid commissure as in *Elops* (Nybelin, 1967), as well as along the anterior border of the orbit in *Osteoglossum* (Taverne, 1977), strongly suggesting the homology of these canals to the anterior and posterior lateral commissures respectively. An ethmoid commissure is lacking in most teleosts, but is represented as a line of neuromasts in many percomorphs (Freihofer, 1978).

Postorbitally, the supraorbital canal of actinop-terygians primitively continues virtually to the rear margin of the cranial roof without communication to the infraorbital or otic canals, although the transverse otic pit line in some Bear Gulch actinopterygians may completely span the gap (Lowney, in press). An anterior extension of the postorbital branch of the infraorbital canal in the position of the epibranchial line can be found in some Paleozoic actinopterygians and in one Bear Gulch taxon "long pelvic" (Lowney, in press) it is continuous between supraorbital and otic canals. There is no evidence to indicate whether this is the principal pathway by which connections between supraorbital and otic canals evolved in more derived actinopterygians, as the supposed epibranchial line is invariably found in a single, highly specialized anteriorly extended postorbital (dermosphenotic) bone. Among teleosts, the

supraorbital canal may end blindly without communication with the otic canal (*Hiodon,* Taverne, 1977) or course directly into the otic line at the level of the transverse supraorbital commissure (*Osteoglossum,* Taverne, 1977). This level of difference within an order of teleosts requires that the primitive condition for the ancestry of the teleosts retain at least the genetic capacity to generate both pathways.

The infraorbital canal in coelacanths curves upward behind the orbit, intersects the jugal line and then courses dorsally as the postorbital line (Fig. 43). The jugal canal meets the preopercular canal in a T-shaped intersection in *Polyosteorhynchus* and *Rhabdoderma* (Figs. 4, 54A), relatively low on the cheek but dorsal and well posterior to the quadratojugal pit line. The preopercular canal extends dorsal to the intersection before ending, usually accompanied by a prominent pit. There is no dorsal communication with the otic canal. In the rhipidistians, the main canal of the cheek courses posteriorly and then ventrally to join the mandibular canal, and is usually associated with the quadratojugal pit line in the same manner as in the coelacanths. The canal thus seems to be composed of the jugal plus the ventral end of the preopercular canal, with no indication of dorsal portion of the preopercular canal (Fig. 76). One porolepiform, *Holoptychius flemingi* (Jarvik, 1972), displays a short ventral canal through the prespiracular bone suggestive of a possible dorsal connection between otic and preopercular canals (Fig. 76D), but no close association is developed. In dipnoans, adults display a pattern of lateral line canals in the cheek as in crossopterygians (Figs. 76C, F), but early embryonic stages of *Epiceratodus* reveal a vertical preopercular canal in contact with the otic canal dorsally (Greil, *in* Stensiö, 1947), ontogenetically reinforcing the hypothesis that the dorsal limb of the preopercular canal is phenotypically suppressed prior to or during the early evolution of Dipnoi and Crossopterygii.

The primitive condition in the Paleozoic actinopterygians is as in the model, where the vertically oriented preopercular canal communicates between the mandibular canal ventrally and the otic canal posterior to the postorbital intersection (Stensiö, 1947; Lowney, 1980). Among the Paleozoic actinopterygians, only *Phanerosteon* is known to retain a complete jugal canal as well as a strong remnant of the quadratojugal canal (Lowney, 1980). In many Paleozoic actinopterygians only a small pit line remains of the jugal (or supramaxillary) line, and a secondary connection between preopercular and postorbital canals is acquired ventral to the intersection of postorbital and otic lines (Moy-Thomas and Miles, 1971). The condition of the preopercular and postorbital canals in the teleosts conforms to that of the most primitive actinopterygians, although only an occasional pit line remains of the jugal canal. It should be mentioned that in both the Chondrichthyes and the Acanthodii (Stensiö, 1947) the preopercular and postorbital lines separately connect to the otic canal, and a canal interpretable as the jugal canal is present.

It must be concluded that the pattern of lateral line canals in the Osteichthyes corresponds closely in details to that of the model (Fig. 73), and is sufficiently conservative to provide a basis for judgements of primitiveness and of homologies.

The lateral line canals of the antorbital region of the hadronectoroidean coelacanths retain a more primitive condition than that known in any other osteichthyan. The condition of the supraorbital-otic canal area in the Bear Gulch hadronectoroid coelacanths is less primitive than that of either the most primitive known dipnoan or actinopterygian conditions. The pattern is clearly more primitive than either porolepiform, osteolepiform, or onychodontiform conditions. Further, the more derived coelacanths display a pattern convergent upon the osteolepoid condition, as well as that of the more derived dipnoans, but there is reason to suggest that the porolepoid condition represents a separate derivation. The canal pattern of the cheek of coelacanths is slightly more primitive than the ontogenetic expression of dipnoan and rhipidistian cheeks, approaching the primitive condition as expressed in the Paleozoic actinopterygians and present in the early ontogeny of the dipnoan *Epiceratodus.*

EXTERNAL BONES OF THE HEAD

The cranial osteology of coelacanths is the final ontogenetic expression of three apparently separate anatomical systems, the lateral line, the external "ornamental" skeleton, and the basal bones, interrelated through developmental processes that are still only poorly understood. It is clear that lateral line canal bones may ossify through the fusion of several bone primordia, each primarily associated with a neuromast (for example, Pehrson, 1947). It is also clear that lateral line canal bearing bones seem to be as subject to gross individual variation (Jarvik, 1948; Jollie, 1980; Parrington, 1949; Miles,

1977) as "anamestic" bones. Ontogenetic and phylogenetic pathways of the odontodes or odontode layers also coincide to a greater or lesser extent with those of the deeper mesodermal bone (*Hadronector*, see Lowney, 1980; Ørvig, 1975). Development of the bones of the skull additionally may be subject to modification in response to shifting mechanical stresses from genetically unrelated anatomical systems, a topic virtually unexplored in fish but actively explored elsewhere. Therefore, decisions on bone homologies and phylogenetic implications, when made without realization of the potential complexities of these factors, can prove quite misleading. The Bear Gulch coelacanths cast some new light upon the developmental aspects as well as the basic pattern of coelacanth osteology, and by extension into the basic interrelationships of the Osteichthyes.

Supraorbital canal bones.—The condition of the bones of the dorsal aspect of the head that most closely approximates the model of the primitive lateral lines is seen in *Dipnorhynchus sussmilchi* (Fig. 76F), where the supraorbital canal lies under the centers of the middle of three paired series of bones from the rostral region to the rear of the skull (the series Q, M, L, K, J3, of Westoll, 1949). The most mesial series of bones lacks a lateral line canal as far forward as can be resolved and contains only one large paired element, and the lateral series consists of apparently non-canal bearing supraorbitals followed by a series of four bones carrying the otic canal (the series 4, X, Y_1, Y_2 of Westoll). The smaller bones in each longitudinal series correspond to each other more or less precisely in transverse rows. Among the Hadronectoroidei, the general pattern consists of three longitudinal series from the anterior end to the rear margin of the skull. Anterior to the intracranial joint differences occur in that both the lateral and the central series participate in the pore system of the supraorbital canal (*Polyosteorhynchus, Allenypterus,* Fig. 75B), and that in all coelacanths there is an additional large element in the most mesial series anterior to the intracranial joint, the parietal. *Allenypterus* displays late ontogenetic fusion of the middle to the most mesial series, *Hadronector* shows fusion of elements of the lateral supraorbital series, and all other known coelacanths except *Euporosteus* (Fig. 75A) have only two series of longitudinal elements, the consolidation of middle and mesial series evidently taking place in early ontogeny.

All coelacanths display only two series of bones posterior to the intracranial joint, a derived con-

dition. Further, the otic series, the supratemporal and tabular, consists of fewer bones than in *D. sussmilchi* and reduction of the supratemporal bone in the coelacanths results in either its elimination (*Latimeria*) or possibly fusion of the middle series in Dipnoi with the most mesial element (B_2 of Westoll).

Osteolepiformes and Onychodontiformes have only two series of elements, the supraorbital canal passing from the nasal series most anteriorly into the mesial element over the orbit, then laterally again postorbitally. The most posterior element in the middle series bears transverse and posterior pit lines, has been called the postparietal and seems to be comparable in detail with the postparietal of coelacanths. A non-canal bearing bone, the extratemporal, is found lateral to the tabular of *Osteolepis, Porolepis* and *Onychodus* (Andrews, 1973), that is not found in coelacanths. The one or two supraorbitals in Osteolepiformes lack canals.

The rostral region of *Holoptychius flemingi* consists of a large and variable number of bones in a mosaic relationship to each other (Fig. 76D), and a variable pattern of branching of the lateral line canals. Comparison of this region with other crossopterygians is made difficult because of bone growth and overgrowths of cosmine; both *Eusthenopteron* (Fig. 76E) and *Strunius* (Jessen, *in* Moy-Thomas and Miles, 1971) have relatively few, large bones in the same area, but the patterns seem to differ. Dipnoans as well generally have solidly ossified rostral areas, but *D. sussmilchi* (Miles, 1977) and *Uranolophus* (Denison, 1968) show traces of mosaic ossification in this region.

Accepting the concept that the basal gnathostome condition may be typified by an acanthodian-like state of many small dermal elements, the holoptychiid and dipnoan condition may represent the most primitive known in the Osteichthyes, although details are absent. Posterior to this region, however, although *Holoptychius* has several more supraorbital bones than any osteolepiform, neither *Holoptychius* nor *Porolepis* has a clear indication of either middle or lateral bone series except for the tabular and an extratemporal ossification. The supraorbital canal continues into the postparietal, and the otic canal is represented only by a short segment in the tabular.

The published actinopterygian condition is never seen to consist of more than two longitudinal series of bones, the supraorbital canal being associated with the mesial series; except in *Acipenser* where

three series are present in the supraorbital region and the canal is generally associated with the middle series (Jollie, 1980; but see Jarvik, 1948, for variations). A large and variable number of bones are found in the rostral region, but not associated with lateral line canals. The signficance of the osteology of *Acipenser* is uncertain, but the pattern of bones of the supraorbital canal in published Actinopterygii is clearly derived relative to the coelacanths.

A pair of very small series of bones at the anterior end of the supraorbital canal of Hadronectoroidei seem to represent ossifications of the antorbital and the anterior lateral commissures. They may be equivalent to the frontonasals or tectals of *Eusthenopteron* (Fig. 76E) or some of the series of small elements in *H. flemingi* (Fig. 76D), and in turn to the anterior supraorbital canal elements in "worm fin" (Lowney, in press) among the Actinopterygii, but in no case can the requisite canals be demonstrated that would establish direct relationships. At present this condition among the coelacanths must be considered as primitive for all Osteichthyes. The loss of these canals and bones in the Coelacanthoidei, therefore, would constitute a set of derived states.

Anterior infraorbital canal bones.—The ethmoid commissure is carried in association with the rostral bone in known primitive coelacanths. It is felt that this small element and the associated canal are more likely to be missed in the specimens than to be absent from the species in which they have not been reported. The rostral of the hadronectoroids and *Rhabdoderma* separates the premaxillae in the midline, but is not toothed. *Holoptychius flemingi, Eusthenopteron,* and Onychodontiformes are reported to have a small median rostral, which does not separate the premaxillae in the midline. The ossified dipnoan anterior region is not comparable. A small, separate, canal carrying rostral bone, bearing teeth, is also considered the primitive condition in Paleozoic actinopterygians by Lowney (1980, in press), who has found no evidence for the previously reported "rostropremaxilloantorbital" of Gardiner (1963) in any actinopterygian. With the exception that the rostral of coelacanths does not bear teeth, the coelacanth and actinopterygian condition is considered primitive, without being able to evaluate the lungfish.

A series of anterolateral rostrals is present in Hadronectoroidei, followed by a prominent posterolateral rostral in all coelacanths. Reduction in numbers or elimination of the anterolateral rostrals would constitute a series of derived character states.

The posterolateral rostral of all coelacanths has a distinctive morphology relating it not only to the infraorbital lateral line canal but to the (topographically) anterior naris, and indirectly to the presence or absence of choanae. There is a bone in *Holoptychius flemingi* closely resembling the posterolateral rostral (Fig. 76D), and there is a virtually identical bone in the Devonian Gogo onychodontid (Andrews, personal communication). No other known osteichthyans have a bone appearing in any way to be similar. The anterior portion of the infraorbital canal is supposedly carried in the premaxilla of all known rhipidistians, a clearly derived condition (Pehrson, 1947) relative to the coelacanths. Among actinopterygians, only the recent *Elops saurus* has separate anterolateral rostrals (Nybelin, 1956), whereas virtually all others carry the anterior portion of the infraorbital canal in a single antorbital bone that may represent the fusion of the coelacanth lateral rostrals, antorbital and anterior part of the lacrimojugal. The condition in most actinopterygians is derived relative to the coelacanth condition. In *Allenypterus, Hadronector,* and probably *Polyosteorhynchus,* there is evidence for a series of bones between the supraorbital canal series and the infraorbital canal series, associated with the posterior lateral commissure and the posterior pores of the rostral organ. The loss of these bones, and the loss or modification of the canal organs, would constitute derived states. The rhabdodermatids retain only the antorbital bone, whereas coelacanthids eliminate this element as well.

There are considered to be two external narial openings as a primitive condition in all Osteichthyes, although the position of the nasal capsule varies from ventral in dipnoans to ventrolateral in coelacanths and crossopterygians to dorsolateral in actinopterygians. From the standpoint of morphological and functional complexity, a secondary association between the flow across the olfactory membrane and flow of respiratory water into the mouth has arisen several times within the gnathostomes. The suggestion of Andrews (1973), therefore, that the absence of a choana in Onychodontiformes and Coelacanthiformes may be a secondary loss, may be the least parsimonious hypothesis. An objective position on this question, however, is difficult to state, just as is an objective position on a number of other critical distinguishing absences in the coelacanths such as cosmine, a maxilla, and a supraotic cavity (Miles, 1977).

A series of large median postrostral elements is

found only in *Hadronector, Diplocercides,* and *Euporosteus* among coelacanths. In other coelacanths, a large element called the postrostral is associated with the anterior end of the frontonasal series and pores of the supraorbital canal (or antorbital commissure). It may be a fusion of several paired elements, thus not strictly homologous with that of *Hadronector.* There is very little basis for assignment of directionality to evolutionary trends in these elements aside from their reduction or absence in other coelacanths. Only *Holoptychius flemingi* shows bones in this area among crossopterygians, and it has four small bones (Jarvik, 1972); other crossopterygians and dipnoans do not reveal separate ossifications.

Actinopterygians generally have a single postrostral, that may fuse to the rostral in some lines, though *Cheirolepis* (Watson, 1925) is restored with two median postrostrals. It shall be assumed that the presence of several postrostrals is primitive and their absence a derived condition.

A premaxilla is apparently present in all osteichthyans, and is found in several different states among coelacanths. It may be justifiable to assume that a simple toothed strip, perhaps with a slight dorsal lamina, represents the primitive state, as in *Allenypterus,* and that emargination of the dorsal lamina and perforation of the dorsal lamina for a pore represent separately derived conditions. The latter state is confined to a small assemblage of Carboniferous forms assigned to the Rhabdodermatidae. Dipnoans have a vague dentigerous "upper lip" (Denison, 1968; Bernacsek, 1977) fused to the remainder of the snout region. Osteolepoids, porolepoids, and onychodontoids have a premaxilla fused to the anterior infraorbital canal as does *Polypterus,* where the condition has been demonstrated to be secondary (Pehrson, 1947). The primitive actinopterygian condition is that of a toothbearing element with a dorsal lamina, not associated with a canal or fused with any other bones and separated in the midline by a rostral (Lowney, in press). The actinopterygian and coelacanth conditions are equally primitive as far as the data permit evaluation.

Posterior infraorbital canal bones; bones of the cheek.—All known coelacanths carry the infraorbital canal around the orbit through two bones, the lacrimojugal and the postorbital. Osteolepiformes, Porolepiformes, and Onychodontiformes all have three bones in the series, the lacrimal and jugal being separate ossifications. *Dipnorhynchus* has five bones, *Dipterus valenciennesi* has five or six bones, and

most Paleozoic actinopterygians have two bones that do not correspond topographically to the coelacanth elements. Modern teleosts and two Bear Gulch actinopterygians have five or more elements. While there is no reason to agree upon a primitive number of elements in the series, the number apparently was higher than the two found in coelacanths.

The preopercular canal of *Rhabdoderma* and *Polyosteorhynchus,* among other coelacanths, courses through two bones between the mandible and the intersection with the jugal canal, the preoperculum and squamosal, as may the canal of *Nesides heiligenstockiensis* (Jessen, 1973). This is interpreted on present evidence as being the primitive condition for the order. Alternatively derived conditions include the reduction of the preoperculum with capture of the canal by the quadratojugal in *Whitea* (Lehman, 1952), the apparent elimination of a ventral bone in the series in "*Diplurus*" (Schaeffer, 1952), or the reduction of one or both of the bones to thin osseous tubes as in *Coelacanthus granulatus* (Schaumberg, 1978). The osteolepoids are similar to the coelacanths in number and position of the bones and canals. The Porolepiformes have three bones in the preopercular-jugal canal series, and no indicators of where, if at all, the two canals might have joined (see Stensiö, 1947). Further, *Holoptychius flemingi* is credited with a small dorsal branch of a canal in the prespiracular bone (Fig. 76D). There are four or five bones of the preopercular canal in early Dipnoi (Westoll, 1949; Miles, 1977). Among the Actinopterygii, there are two bones that carry the canal between mandible and otic canal, occasionally a third, equivalent to the postsubmandibular of Porolepiformes (Lowney, in press; Lund, in manuscript) and indications of a complete mandibular operculum dorsal to the articular. The jugal canal, although complete in only one Bear Gulch actinopterygian, *Phanerosteon,* crosses an additional bone between the preoperculum and the infraorbital line. There is therefore, evidence that at least four bones may have been primitively involved in the preopercular and jugal canals in the actinopterygian and dipnoan conditions, reduced somewhat in the coelacanths. There is also evidence for a complete mandibular operculum as the primitive osteichthyan condition. The pathways and phenotypic expressions of the lateral line canals of the cheek are complex and should not be considered as a single character state.

The Porolepiformes and *Dipnorhynchus* have four additional bones in the cheek, the two called the

prespiracular and quadratojugal in porolepoids not necessarily corresponding to bones in the cheek of lungfish. The coelacanths have elements that may reasonably be called prespiracular and quadratojugal but lack any other cheek bones; *Osteolepis* lacks a prespiracular, as may *Eusthenopteron,* which is a derived state relative to dipnoans, porolepiformes and coelacanths. The prespiracular and ventral preoperculum (postsubmandibular) are reasonably stated to be derivatives of the dorsal half of the mandibular operculum (Jarvik, 1963). No dipnoan has a spiracle, nor a prespiracular, but several taxonomic groups among the Bear Gulch actinopterygians retain various stages in the reduction of the dorsal part of the mandibular operculum to the relatively derived stage present in porolepoids.

The mandibular lateral line canal in coelacanths is carried in two bones, the angular and the "splenial," or anterior infradentary. *Dipnorhynchus* among the dipnoans, as well as *Holoptychius* and *Eusthenopteron,* carry the mandibular canal on a chain of infradentaries, a more primitive state than the coelacanth condition. Actinopterygians are separately derived in carrying the canal on two bones, the largest of which is the dentary (Lowney, 1980), the sole anterior lateral bone of the lower jaw.

The dentary is a small element at the anterodorsal margin of the lower jaw in most coelacanths. It is proportionately longer in *Polyosteorhynchus* and *Lochmocercus,* and even more so in young individuals of the former genus. The occlusal line of the dentary continues smoothly back to the coronoid eminence of the angular in these two forms, a condition that corresponds with the occlusal line of other osteichthyans and can be accepted as primitive. Miles (1977) also convincingly argues that a longer dentary can be accepted as primitive for both coelacanths and dipnoans. The anterior angular diastema in the occlusal line of most later coelacanths (*Caridosuctor,* Fig. 21), and the strong angulation between the dentary-splenial and the angular portions of the jaw are considered derived conditions, the latter of which seems to have been very variable among coelacanths (Schaeffer, 1952). The diastema may be associated with the development of the maxillolabial ligament in *Latimeria* (Millot and Anthony, 1958). There seems to always be a complete series of vaguely defined coronoid elements from an adsymphysial plate to the uniquely enlarged coronoid of coelacanths, although the angle, dentition and relationships of the coelacanth element here termed precoronoid is quite varied. The presence

of this series seems to be primitive for osteichthyes (Miles, 1977), although the coelacanth coronoid is a uniquely derived modification. The supposedly triangular coronoid mentioned in some coelacanths is probably an artifact of observation, although coronoids do differ in shape of the dorsal edge, position and dentition.

No coelacanth has a maxilla. Coelacanths share this condition only with dipnoans. It is not possible to determine the primitive state of the posterodorsal margin of the mouth on the basis of objective criteria for coelacanths, but there seems to be some reason to believe that the condition is primitive for dipnoans. It may be presumed, for argument, that the lengths of the dentary and maxilla closely correlate for functional reasons in primitive rhipidistians and actinopterygians. A relatively long dentary in occlusal line with the enlarged angular seems to be primitive for coelacanths (see above). This suggests that very different stress distributions were present in the most primitive coelacanths like *Lochmocercus* and *Polyosteorhynchus* and strongly suggests derivation from an ancestor that transferred biting forces along the lateral aspect of the jaw as well as weaker forces along the prearticular. We feel that the lack of a maxilla in coelacanths is a uniquely derived feature.

The palates of coelacanths are all very similar in osteology and articulation. There is a well developed autopalatine, anteroventrally fringed with tooth plates in the position of a dermopalatine. The vaguely defined dermopalatine tooth patches form a continuous line of fine teeth between vomers anteromesially and the thin ectopterygoid along the lateral edge of the endopterygoid, the principal bone of the palate. The absence of a well defined dermopalatine may be a primitive condition. The posterodorsally placed metapterygoid (epipterygoid) articulates with a well developed antotic process in all known coelacanths, although the antotic of hadronectoroids may project as far laterally as posteriorly to the intracranial joint. There is no evidence for a basipterygoid process in any coelacanth but Diplocercides (Bjerring, 1973); the absence of this articulation is considered a derived character among coelacanths (Andrews, 1977).

As far as can be determined, no coelacanth has well developed pharynogobranchial elements or unspecialized epibranchial elements. They are thus uniquely derived among the major taxonomic groups of gnathostomes in this regard.

The primitive condition of the opercular series

among known coelacanths is to have both an oper-
culum and a subopperculum, but to lack a branchios-
tegal series between the subopperculum and the gular
plate, as in Hadronectoroidei. No other coelacanths
have a bone with the distinctive morphological re-
lationship to the operculum that a subopperculum
must have except perhaps *Nesides? heiligenstock-
ensis* (Jessen, 1973). All Coelacanthoidei are derived
in this character state. All Coelacanthiformes are
derived in the lack of branchiostegal rays, a median
gular or submandibular bones relative to dipnoans
and crossopterygians. Dipnoans share with coel-
acanths a marked reduction in the branchiostegal
series (Miles, 1977). The actinopterygians lack a
submandibular series related to the lower jaw, and
only occasionally have lateral gulars; the former is
derived state, whereas the second is primitive in
relation to the remainder of the Osteichthyes (Low-
ney, 1980).

Shoulder Girdle

A bony attachment of the dorsal end of the shoul-
der girdle to the skull roof is rarely well preserved
among coelacanths and seems to be absent in most,
a presumably derived condition relative to the re-
mainder of the Osteichthyes. There is a suggestion
of a stout, anteriorly inclined element in *Diplocer-
cides* and *Lochmocercus* that may have fulfilled this
function in a manner similar to that of the remaining
crossopterygians; this is considered here as primi-
tive. Vertical, spike-like anocleithra as in *Polyosteo-
rhynchus,* short, blunt vertical elements as in the
Rhabdodermatidae, or S-shaped elements as in *Al-
lenypterus* and *Hadronector,* none of which have a
bony anocleithral spur to the braincase, are consid-
ered as derived conditions. *Macropoma* (Fig. 75F),
however, has both an anterior process and a vertical
process, which may be a secondary condition.

Extended anteroventral processes of the cleith-
rum and posterodorsal processes of the clavicles,
associated with a loose, large extracleithrum are the
derived condition among coelacanths, as found in
Allenypterus and Rhabdodermatidae. The presence
of the extracleithrum itself may be very difficult to
demonstrate if all elements of the shoulder girdle
are tightly associated, as in *Lochmocercus,* primitive
dipnoans, crossopterygians and actinopterygians.
The structure and function of osteichthyan shoulder
girdles needs considerably more analysis before the
details can be used in any evolutionary schemes.

No coelacanth has an interclavicle, a condition
that agrees with that of onychodontoids (Andrews,

personal communication) and actinopterygians.
Primitive dipnoans, porolepoids and osteolepoids,
have an interclavicle (Andrews, 1977), a condition
that has been interpreted as primitive (Andrews,
1977).

Postcranial Skeleton

All well preserved coelacanths share the uniquely
derived ossified swim bladder wall.

All well preserved coelacanths have numerous
sclerotics, a character they share in common with a
diverse assortment of totally unrelated gnatho-
stomes (Miles, 1977).

Pelvic girdles are primitively located near the rear
of the peritoneal cavity, as in *Allenypterus* and other
osteichthyans. The derived condition as found in
other Hadronectoroidei is a midabdominal location
of the pelvics, while this condition is complicated
in the Coelacanthoidei by the rearward inclination
of the first haemals and freeing of the anal fin sup-
port from the first haemals. The pelvic plates are
primitively simple and triangular (*Allenypterus*), and
secondarily quadrangular (*Lochmocercus*) or elon-
gate (*Polyosteorhynchus*) plates not articulating
across the ventral midline, as in other osteichthyans
(Rosen et al., 1981). *Hadronector* shares with the
Rhabdodermatidae and some other coelacanths the
more highly derived condition (Figs. 35, 74). *Laugia*
and *Allenypterus* have linked the pelvic girdle to the
shoulder girdle by entirely different specializations.
The pelvic plates of crossopterygians and dipnoans
are poorly represented, but separate, triangular plates
in osteolepoids (Andrews and Westoll, 1970a, 1970b)
are found. In dipnoans there is a single, median plate
(Miles, 1977), while the minimal data available for
actinopterygians also indicate paired, simple trian-
gular plates (Lowney, 1980).

The paired fins of the Bear Gulch coelacanths add
no useful information to what is already known.
Both pectoral and pelvic fins are lobed, borne upon
an endoskeletal axis articulated to the scapulocor-
acoid by one radial, branched distally, and exter-
nally scaled and muscularized (Andrews and Wes-
toll, 1970a, 1970b). They share this character with
all known Crossopterygii (except that the porolepi-
form axis is presumably secondarily unbranched;
Andrews, 1973) as well as with dipnoans. They differ
strongly from the actinopterygian paired fin sup-
ports, which consist of a single row of segmental
radials. It is presumed that the actinopterygian con-
dition is primitive (Goodrich, 1930).

The first dorsal fin support of coelacanths consists

of a basal plate articulating directly, as far as is known, with serially arranged fin rays. The first dorsal fin support of the known crossopterygians (Andrews and Westoll, 1970a) has at least one distal row of radials, while dipnoans and actinopterygians primitively share a segmentally arranged median fin supported by rows of supraneurals (epineurals), baseosts, and axonosts (Obruchev, 1967; Lowney, 1980).

The second dorsal fin of *Latimeria* is supported by a basal plate with a long anterior process, a thin ventral process and a posterior articulation with branching, jointed radials (Andrews, 1973). In hadronectoroids and *D. huxleyi* there is no anterior process and the plate itself is rounded and almost directly under the fin. There are no preserved distal elements in fossil coelacanths. In *Eusthenopteron* and osteolepids, there is a single, slightly distally expanded proximal element followed by two series of more distal radials. In Porolepiformes there is a large plate serially homologous with epineurals, followed by two to three serial rows of radials distally (Andrews and Westoll, 1970a, 1970b). It seems most conservative to accept three rows of elements distal to the neural spines as primitive, and consider the porolepiform condition secondarily modified, as are the paired fins.

The anal fin supports of coelacanths primitively consist of a single basal plate supported dorsally from the first two haemal spines, as in Hadronectoroidei. *D. huxleyi* shows an anterior shift of the distal end of a basal plate shaped very much like that of the osteolepoids, while retaining the proximal support upon the haemal spines; Rhabdodermatidae show, as far as the elements ossify, a simple rod in the ventral body wall, while Coelacanthidae have accessory processes on the free ventral anal support (Schaeffer, 1941). The anal fin support of other Crossopterygii consists of a narrow plate plus two series of distal radials, that of the osteolepoids supported below the first haemals while that of the porolepoids is secondarily located behind the first complete haemal. Anal fins of dipnoans and Actinopterygii are supported upon serially arranged infrahaemals, baseosts and axonosts, considered to be the primitive condition. It should be noted that with the exception of the Porolepiformes second dorsal plate, the median fin supports of all crossopterygians are homologous with single epineural or infrahaemal elements, in strong contrast to the dipnoan and actinopterygian conditions.

All coelacanths have the neural arches and spines fused into a single, median structure. In contrast, the most anterior trunk neural elements in osteolepoid and porolepoid fish may be unpaired (Andrews and Westoll, 1970a, 1970b), and there are suggestions that the anterior neural elements may not have fused in some dipnoans (Obruchev, 1967). The primitive actinopterygian condition is paired, unfused neural arches and spines (Lowney, 1980), a condition that is also primitive for the chondrichthyan axial skeleton. A clear series of specialized cervical neural arches, as seen in all Bear Gulch coelacanths, is similar to the condition in *Latimeria* (Andrews, 1977). Preservational deficits make the cervical region an inaccessible character in most species.

The external shape of the tail of coelacanths is diphycercal, with an extended caudal lobe and tuft. The terminal caudal lobe and tuft are present as an adult character in Onychodontiformes, other juvenile crossopterygians (Schultze, 1973; *Miguashaia* has no unique coelacanth characters, either illustrated, described, or implied), all Bear Gulch actinopterygians in which preservation allows the determination (Lowney, 1980), juvenile *Lepisosteus* (Schultze, 1973), and the crank shaped tail of developing teleosts (Westoll, personal communication), and therefore must be considered primitive for the Osteichthyes irrespective of the angle of the body axis or the shape of the caudal fin itself. The shape of the caudal fin, whether rounded, elliptical, or square eut, is a highly adaptive character (Lund et al., in press; Dicanzio, in press) related to acceleration, aspect ratio, and drag (Alexander, 1973), and cannot be used in analysis of relationships among distantly related and ecologically isolated fish. Of considerably more pertinence are two other features, heterocercality and the symmetry of internal structure. On the symmetry of internal structure, endoskeletal supports of the caudal fin are more or less symmetrical across the axis in coelacanths, with as great an epichordal component as a hypochordal component. There is one row of well developed endoskeletal supports distal to the neural and haemal spines in all, including the asymmetrical and highly derived *Allenypterus*. In all crossopterygians where the endoskeleton is known, a series of supports distal to the axial spines can be found only hypochordally, although there are precaudal epineurals in porolepoids (Andrews and Westoll, 1970a), a derived condition. The presence of free caudal epineurals would indicate that the diphycercal condition is primitive, as in coelacanths, whereas their absence would in-

dicate secondary diphycercality, as in *Eusthenopteron* (Obruchev, 1967). The endoskeletal supports for the caudal fin of Onychodontiformes are unknown, but there seem to be no substantive differences between the condition in *Strunius* (Andrews, 1973) and that in coelacanths. Dipnoi are said to have up to three rows of distal radialia (Obruchev, 1967), although details are lacking in most lungfish. There is a single series of epichordal radials anterior to the caudal fin in occasional teleosts (J. Dooley, personal communication), although none are reported in the fossil record. Distal radials of the hypochordal lobe of Actinopterygii are rare, quite reduced and not continuous to the end of the haemal series (Lowney, 1980). It has been accepted virtually without question that the heterocercal tail is primitive for bony fish (Andrews, 1973, for instance) and probably for gnathostomes, simply because of its prevalence (Romer, 1966), but this hypothesis introduces difficult evolutionary problems with regard to the internal structure of the tail. Clearly, in all cases of heterocercal tails, the distal epichordal radial series is absent or unossified. It is very unlikely to expect that distal radials would reappear in a secondarily diphycercal tail separated from influence of an also secondarily elongate dorsal fin, and indeed they do not. One is therefore forced to accept either that the diphycercal tail with unreduced epichordal components is primitive, and heterocercal tails arose several times in parallel, or that distal epichordal elements arose anew in some, but not all, diphycercal tails. Considerations of the Chondrichthyes in this situation do not clarify or strengthen the primitiveness of the heterocercal tail and suggest that the primitive condition of the chondrichthyan caudal is also internally symmetrical. While there is presently no elegant solution to this question, we assume that the coelacanth condition is derived relative to reputed dipnoans with more than one row of distal elements, and primitive relative to the crossopterygians as well as the actinopterygians.

A greater number of fin rays than endoskeletal supports is said to be primitive for coelacanths (Stensiö, 1937), while the presence of branched fin rays is said to be primitive for crossopterygians (Andrews, 1973). The fin rays of Dipnoi are not bony (Obruchev, 1967) but cartilaginous, while the fin rays of actinopterygians are bony but do not necessarily show any clear relationship between branching and any evolutionary tendencies (Lowney, 1980). The primitive coelacanth condition of fin ray numbers in the median and paired fins is derived relative both to the primitive condition in Crossopterygii and Actinopterygii, whereas the dipnoan condition appears to be a separately derived condition, from a crossopterygian-like condition (Denison, 1968).

All coelacanth scales are cycloid and ornamented with lines of enameloid on the posterior field, also a derived condition relative to the apparent primitive condition of other Osteichthyes. The absence of cosmine in coelacanths and actinopterygians is troublesome; Miles (1977) assumes for simplicity that the presence of cosmine is a shared, derived character among primitive crossopterygians and dipnoans, its absence primitive in coelacanths and actinopterygians. There seems to be little firm ground for a decision on this character in light of the trends among coelacanths for reduction of ornamentation and the separate origin, somewhere within the coelacanths, of a unique sensory system, the rostral organ, that may imply divergent sensory specializations among the early Osteichthyes.

INTERRELATIONSHIPS OF THE GROUPS

It is plausible to draw conclusions about the directionality of many characters among the coelacanths from the foregoing comparisons—several of these are embodied in Table 7. Several features of this comparison however are made difficult by the absence of relevant information among published accounts of many coelacanths. The resultant scheme of possible relationships is not aided by the observation that the Bear Gulch coelacanths, while divergent from even the Devonian Diplocercidae, are collectively more primitive in all useful character states than all other known coelacanths. The resultant scheme of relationships thus is a series of levels of change, or grades of evolution, in which there are virtually no conclusive connecting links between grades. Even within the Hadronectoroidei it is not possible to demonstrate any single preferable grouping of interrelationships or ordering in a single most parsimonious scheme.

Among the Devonian and Carboniferous coelacanths for which even a modicum of useful information is available, it is only possible to say that

Table 7.—*Comparisons of character states among coelacanths. Abbreviations: Am, Allenypterus, Ps, Polyosteorhynchus; La, Lochmocercus; Hd, Hadronector; C-R, Rhabdodermatidae; D, Diplocercides (after Stensiö, 1937); E, Euporosteus (Stensiö, 1937); Du, Dumfregia; Cg, Coelacanthus granulatus (Moy-Thomas and Westoll, 1936, Schaumberg, 1978); W, Whitea (Lehman, 1952); Un, Undina (from Schaeffer, 1941, 1952); M, Macropoma (Watson, 1921); Ax, Axelia, Mylacanthus, Scleracanthus (Stensiö, 1921); Di, Diplurus (Schaeffer, 1952); L, Latimeria (Millot and Anthony, 1958); D^{1-n}, derived character states 1 through n, usually implying a continuum; D^9, separately derived state, P, primitive. Refer to text for discussion.*

Characters	Am	Ps	La	Hd	C-R	D	E	Du	Cg	W	Un	M	Ax	Di	L
Premaxilla	P	D^1	?	D^1	D^9	?	?	?	P	D^2	P?	D^2	D^2	P?	P?
Mesial supraorbital	P	P	?	D	P	P	P	D	D	D	D	D	D	D	D
Lateral supraorbital	D^1	P	D^2	D^9	D^2	D^2	P	D^2	D^2	D^2	D^2	D^2	D^2	D^2	D^2
Anterolateral rostral	P	P	?	P	D^1	?	?	?	?	?	?	?	?	?	P?
Antorbital	P	P	P	P	P	P	?	P	D	P	P?	D	D	D	D
Extra snout series	P	P	?	D^1	D^2	?	?	?	D^2	D^2	D^2	D^2	?	D^2	D^2
Cheek bones	P	P	P	P	P	D	?	?	D	D	D	D	?	D	D
Supratemporal & canal	P	P	D^1	D^1	D^1	D^9	?	?	D^9	D^9	?	P?	?	D^2	D^2
Extrascapulars	P	D^9	P	D^9	P	D^9	?	?	D^1	P	P	D^2	?	D^2	D^2
Dentary	D	P	P	D	D	D	?	?	D	D	P	D	?	D	D
Basipterygoid process	D	D	D	D	D	P	?	?	D	D	D	?	?	D	D
Anocleithrum	D^9	D^1	P	D^9	D^2	P?	?	?	P	D	?	D^9	?	D^1	D^1
First dorsal plate	D^1	D^2	D^2	D^2	D^1	?	?	D^1	D^2	?	D^2	D^2	?	D^2	D^2
Second dorsal plate	P	P	P	P	D	?	?	P	D	?	D	?	?	D	D
Pelvic plate	P	P	P	D^2	D^2	?	?	D^1	D^2	D^2	D^1	?	?	D^2	D^3
Anal plate	P	P	?	P	D^2	?	?	D^1	D^2	?	D^2	?	?	D^3	D^3
Caudal rays	P	D	P	D	D	P	?	D	D	D	D	?	?	D	D

there were two concurrent major groupings. The Coelacanthoidei, represented by the Devonian Diplocercidae, were structurally more derived in most known characters than the Hadronectoroidei, represented by holomorphs from the Namurian Bear Gulch limestone and *Coelacanthopis*. The Devonian *Euporosteus* is known from one isolated ethmosphenoid that may best be assigned provisionally to the Hadronectoroidei on the basis of the multiple series of bones (Fig. 75A). Among other forms assigned to the Coelacanthiformes, *Miguashaia* (Schultze, 1973), as previously discussed, is not a coelacanth. *Chagrinia* (Schaeffer, 1962) shows no diagnostic characters, nor does the unique specimen of "*Coelacanthus*" *welleri* Eastman (1908). Neither the specific nor generic assignment of *Rhabdoderma exiguum* have been confirmed by osteological studies. The putative genus *Synaptotylus* (Echols, 1963) has been in part commented upon by Forey (1981), and his comments on the jaw suspensorium are well founded. The squamosal of "*Synaptotylus*" as illustrated by Echols is extremely close to that of *R. elegans* (Figs. 6–9), but neither this character or any other enable systematic placement to genus to be made. Little more can be said about the British Carboniferous coelacanths assigned to *Rhabdoderma* by Forey (1981) than discussed earlier in this paper; they may be Rhabdodermatidae *sensu stricto* but are not *R. elegans.*

To review the details of Mesozoic coelacanths given in Table 7 would only serve to detail how little is actually known about them. Perhaps the only derived character present in the Bear Gulch coelacanths, including *Caridosuctor,* not present or noticed in other Coelacanthoidei, is that of the cervical neural arch series. Functionally, the cervicals are strongly correlated with the ability to move the oticooccipital moiety of the braincase upon the axis during feeding (Lund et al., in press) and their absence in some species may imply nothing more than subtle differences in feeding mechanism. There is little justification for placing heavy weight on a character where the state of it is unknown in most members of one of the groups.

INTERRELATIONSHIPS OF COELACANTHIFORMES

Among the coelacanths the premaxilla may occur as a toothed strip bearing an undistinguished dorsal lamina, as in *Allenypterus,* which is taken as the primitive condition. Emargination of the dorsal lamina for pores, apparently associated either with the ethmoid commissure or with the rostral organ, is considered a derived character, whereas the perforation of the dorsal lamina for a large pore most

likely associated with the rostral organ, as seen in *Caridosuctor* and *Rhabdoderma,* is considered a separately derived state. The thin toothed strip found in *Coelacanthus, Undina,* "*Diplurus,*" and *Latimeria* may constitute retention or modification from a primitive condition. In *Whitea* (Lehman, 1952) and *Macropoma* (Watson, 1921), the premaxilla has not been found as a separate element, but is reported fused or tightly sutured to the other elements of the rostral region, probably a secondarily derived condition. The two rows of anterior supraorbitals in *Allenypterus, Polyosteorhynchus, Hadronector,* probably in *Euporosteus,* and restored in *Diplocercides,* is considered the primitive state. All other known coelacanths are derived in having a single row of supraorbitals anterior to the orbit. Posterior to the antorbital, *Polyosteorhynchus* maintains two rows of supraorbitals at least to the ontogenetic stages known, *Allenypterus* fuses the mesial row to the medial series in ontogeny, and *Hadronector* fuses the lateral supraorbitals into two elements while retaining some semblance of the mesial series. These are alternative variations upon the primitive condition, which is seen most clearly in *Polyosteorhynchus.* All other coelacanths are derived in having only a single row of supraorbital bones. It should be noted that while in *Allenypterus* the posterior two lateral supraorbitals fuse, there is no significant projection of the supraorbital series posterior to the intracranial joint in either it or *Hadronector* and only slight posterior projection in *Polyosteorhynchus,* probably reflecting the lateral extent of the antotic process. In other coelacanths there is a distinct projection of the last supraorbital posterior to the intracranial joint (Fig. 75).

The presence of several anterolateral rostrals is considered primitive, the reduction to one element, as in *Caridosuctor* and *Rhabdoderma* is derived, and the elimination of this element, where this can be established, is further derived. The presence of a series of bones between the supraorbital and infraorbital canals, extending back to and including the antorbital, is considered primitive for coelacanths, its reduction in *Hadronector* and restriction to a single antorbital in Rhabdodermatidae, *D. huxleyi, Diplocercides,* and *Whitea* a first order derived character, whereas its elimination in *Coelacanthus* and other coelacanths constitutes a secondary derived condition.

Primitively in known coelacanths there is a completely bone covered cheek composed of five tightly abutting or overlapping elements, plus a single lacrimojugal. This is found in all Bear Gulch coelacanths and *Rhabdoderma elegans. Whitea* contains five bones in relatively loose association, with the prespiracular and preoperculum reduced, whereas other coelacanths are reported to have only four bones in various states of reduction, all derivable from a *Whitea*-like state and ultimately from the primitive condition.

A suboperculum, clearly provable by its association with the operculum, is present only in Hadronectoroidei and is absent in all other known coelacanths. The latter condition is derived. The operculum articulates with the tabular in *Allenypterus, Caridosuctor* (but not *Rhabdoderma*), and *Spermatodus* (Westoll, 1939), almost undoubtedly constituting separate derivations in each genus. There apparently were strong selective pressures for this association, possibly linked to the use of opercular pumping in the feeding mechanism (Lund et al., in press).

The otic canal passes between postparietal and supratemporal in *Allenypterus* and apparently in *Polyosteorhynchus,* and in no other known coelacanths. The otic canal occurs within the supratemporal in *Hadronector* and Rhabdodermatidae, and apparently in *Lochmocercus,* and in *Latimeria* passes lateral to the postparietal unaccompanied by bone, as seems to be the case in "*Diplurus*" (Fig. 75E). It has been restored as passing through the lateral margin of the postparietal in *Diplocercides, Coelacanthus granulatus, Whitea,* and *Mawsonia* (Wenz, 1975). While there is little basis for judgment on which condition is primitive, the presence of a supratemporal is primitive, and by extension to the primitive dipnoan condition the path of the otic canal through the most lateral bone series would also constitute the primitive condition. Thus, reduction to elimination of the supratemporal would be one pathway (*Rhabdoderma-*"*Diplurus*"*-Latimeria*) and a relative mesial movement of the canal an alternate derivation (*Polyosteorhynchus-Diplocercides-Coelacanthus*). The utility of this character, however, is severely strained by the speculative nature of the path of the canal in many cases.

The palates of coelacanths seem to vary only in proportions and in patterns of denticulation. Sutures between endopterygoid and metapterygoid generally tend to be either loose or obscured by overlying bone, but the quadrate is virtually never isolated by sutures. The ectopterygoid is present in all

Hadronectoroidei and Rhabdodermatidae, as a thin element that always extends to the level of the middle of the coronoid. There is a thin line of tooth bearing bones, "dermopalatine," under the well developed autopalatine that forms a continuous line between the vomerine teeth anteriorly and ectopterygoid teeth posteriorly. There is no evidence in any Bear Gulch coelacanth for a basipterygoid process, but braincases are not ossified in one piece and are generally collapsed, so evidence in this regard is weak indeed. In terms of braincase, and presumably absent basipterygoid process, the Bear Gulch coelacanths and all others are derived relative to *Diplocercides*.

The lower jaws of most coelacanths are very similar; the characteristic high coronoid, in tight association with the anterior edge of the quadratojugal, marking the corner of the mouth as in *Latimeria*. *Lochmocercus* and *Polyosteorhynchus* are primitive relative to all other coelacanths in lacking a distinct angular diastema, or, expressing the same appearance differently, in having relatively large dentaries on a more or less continuous occlusal line with the angular. In both cases the dorsal margin of the dentary is mesially inset, indicating with the coronoid that there may have been fleshy lips in these species as well. *Lochmocercus* also bears a prominent marginal dentition along the dentary, that can also be considered as primitive among coelacanths.

The extrascapular bones are here considered as all bones bearing the occipital commissure from its intersection with the head canal. As far as is known the primitive number of extrascapulars in coelacanths, and in dipnoans, seems to be five, rather than the three that are primitive for known crossopterygians (Andrews, 1973) or actinopterygians (Lowney, 1980). If this position is taken, *Allenypterus*, *Lochmocercus*, Rhabdodermatidae, and *Whitea* could be considered primitive, although in the case of *Rhabdoderma* and *Whitea* posterior extension of the tabular may have obscured the relationships. Thus, either fewer extrascapulars, as in *Polyosteorhynchus* and *Hadronector*, or more, as is the case in *Coelacanthus granulatus*, "*Diplurus*," *Latimeria*, or *Undina* would potentially be alternate derivations in the absence of convergence. The posttemporal is difficult to detect in many coelacanths because of great reduction in thickness and size, but *Allenypterus* has a posttemporal, albeit small and thin, whereas *Hadronector* and *Polyosteorhynchus* have somewhat more evident posttemporals. If a posttemporal is indeed present in Rhabdoderma-

tidae, it is very small and thin, and does not clearly show a lateral line canal. The evidence for postemporals in most other coelacanths is dubious.

A stout anocleithrum fixed to the skull can be presumed to be primitive. *Lochmocercus* may have this condition, *Macropoma* has it, and as far as can be established, no other coelacanths are primitive in this regard. All others show some reduction of the anocleithrum. The extracleithrum is spotty in its occurrence; preservational factors and functional integration of the clavicle and cleithrum, a primitive condition, tend to obscure its detection. A tightly integrated clavicle and cleithrum, as seen in *Lochmocercus* and *Polyosteorhynchus* (both of which show posteriorly projecting scapulocoracoid ossifications) contrasts with the somewhat looser association seen in *Hadronector* and the highly mobile three bone shoulder girdle of *Allenypterus* and the Rhabdodermatidae, the most derived state. *Diplocercides* and *Diplurus* have relatively tight associations between clavicles and cleithrum, whereas the remainder of the coelacanths seem to have a more mobile arrangement.

The second dorsal fin plates of Hadronectoroidei and *D. huxleyi* are primitive rounded plates with no significant posterodorsal articular facet. Rhabdodermatidae share with all other known coelacanths the derived condition. "*Diplurus*," *Undina*, and *Latimeria* show further derivation in the extreme thinness of the anterodorsal process and in the lowering of several neural spines to either side of the ventral process.

The first dorsal plate rarely shows any ventral processes that suggest fusion from several baseosts. This relatively primitive condition is seen in *Polyosteorhynchus*, *Caridosuctor*, and *Undina*, the remaining coelacanths having a uniform ventral margin.

The pelvic plates of *Allenypterus*, *Lochmocercus*, and *Polyosteorhynchus* are primitively simple, triangular to quadrangular elements lacking significant surficial bone and not bearing a posteromesial articulatory process. The pelvic plates of *D. huxleyi* and *Undina* are thin, elongate structures with weak posteromesial processes at best, whereas those of *Hadronector*, the Rhabdodermatidae, *Coelacanthus granulatus*, "*Diplurus*," and *Latimeria* bear strong articular processes. The pelvic plates of *Laugia* are highly specialized structures. The rhabdodermatid pelvics differ from the coelacanthid condition in having anterolateral rather than anteromesial processes.

The primitive condition of the anal fin support is seen in Hadronectoroidei, where a simple, rounded to elongate basal plate is supported upon a thin stem against the first haemal spine. In *D. huxleyi,* the plate is anteriorly inclined and expanded along its long axis but still braced against the haemal spine. The rhabdodermatid condition is a simple, rarely ossified rod. The anal supports of *"Diplurus"* and *Latimeria* are best described as reclining V's lying free in the ventral body wall, a highly derived condition.

The primitive caudal fin ray : endoskeletal support ratio, approximating 2:1, is found in *Diplocercides, Coelacanthopsis, Lochmocercus,* and variably in *Allenypterus*; all other coelacanths have a derived, 1:1 ratio.

The anatomical information upon which judgements of relationships can be made is scanty for most coelacanths. All coelacanths for which there is adequate information can be separated into two major groups on the basis of characters that mark grades of evolution. All Bear Gulch coelacanths are primitive relative to all others, including the known Devonian forms, in the structure of the cheek. All Hadronectoroidei can be described as primitive relative to all other known coelacanths in having multiple rows of bones in the antorbital region, the relationship of bones to canals in the supratemporal region, the retention of a subopercular, the structure of the second dorsal and anal fin supports, and, with the exception of *Hadronector,* the pelvic plates. Within the Hadronectoroidei, *Polyosteorhynchus* and *Hadronector* share several characters, such as the notched premaxillae, three extrascapulars, 1:1 caudal fin ray ratio, and rounded first dorsal fin plates, that have been interpreted here as being derived, although all are subject to convergence. *Allenypterus* shares derived states of the lower jaw, shoulder girdle and apparent absence of a basipterygoid process with *Hadronector* and most other coelacanths, is uniquely derived in terms of body form and pelvic association, but is primitive in all other states. *Lochmocercus* seems derived in characters of the supratemporal and supraorbital series and the first dorsal fin plate. There are no clear tendencies within the Hadronectoroidei linking any two species.

The Rhabdodermatidae have an assemblage of primitive cheek characters. They have a uniquely derived perforated premaxilla, highly reduced supratemporal, and a derived pelvic plate, but share derived characters of opercular, supraorbital series

bones, and median fin plates with Coelacanthoidei. *Dumfregia huxleyi* could be considered intermediate in known characters between the two major groups.

Diplocercides shares a common derived skull table plan and cheek plan with coelacanthoids, being primitive among all coelacanths in the character of endocranial ossification, basipterygoid process, and caudal fin ray ratio. *Coelacanthus granulatus* is relatively more derived than *Whitea* in cheek reduction, elimination of the antorbital, rostral area reduction, and extrascapular reduction, while being more primitive in posttemporal and supracleithral relationships. *Undina,* which may be an assortment of unrelated forms, has a pelvic plate closely comparable to that of *D. huxleyi* and an apparently primitive number of extrascapulars. *Axelia, Mylacanthus, Scleracanthus, Wimania, "Diplurus"* and *Macropoma* share most derived characters in common with *Latimeria.*

The Mesozoic coelacanths, *Coelacanthus granulatus,* and *Latimeria,* with the possible exception of *Undina,* form a tightly interrelated series of species that could be most easily derived from a *Whitea*-like ancestor. *Diplocercides,* despite its geologic isolation, shares its derived characters with the Coelacanthoidei. Early derivation of many of the characters of the coelacanthoids distinguishes them from hadronectoroids even if classification is limited to Paleozoic forms. Although information is lacking on *Euporosteus* and *Coelacanthopsis,* both may provisionally be included within the hadronectoroids. Classification of *D. huxleyi* must await closer study of its cranial osteology.

CHARACTERS OF THE COELACANTHIFORMES

The unique combination of coelacanth characters can be sumarized as follows—the premaxillae are toothed, do not meet in the midline, and have a low dorsal lamina that may secondarily be emarginated or perforated for pores. There is a small, untoothed median rostral carrying the ethmoid commissure, variably followed by a median postrostral series. Primitively, one postrostral carries the antorbital commissure. Bones of the rostral region may primitively and collectively resemble a mosaic, but all bones are bordered by lateral line canal pores. The roofing bones of the ethmosphenoid moiety of the skull primitively occur in three paired series, the central series overlies the supraorbital canal and the medial series lacks lateral line canal pores, but the central and medial series may fuse. Several antero-

lateral rostrals, a posterolateral rostral, lacrimojugal, and a postorbital bone carry the infraorbital canal, but the anterolateral rostrals may be reduced in number. The posterolateral rostral always bears a ventral prong associated with the anterior external naris. A central series of bones is primitively found between supraorbital and infraorbital canal bones, primitively associated with the posterolateral commissure, but this series may be reduced or eliminated. The cheek bones primitively consist of tightly fit postorbital, prespiracular, squamosal, quadratojugal, and preoperculum. The quadratojugal bears a vertical pit line, the squamosal the jugal canal, and the preopercular canal traverses the preoperculum and the squamosal but is not continuous with the otic canal dorsally. Secondarily, cheek bones may be reduced to canal tubes or individually lost, and the preopercular canal may come to be borne by the quadratojugal. The quadratojugal is always immediately posterolateral to the high coronoid of the lower jaw. The opercular series primitively consists of a large operculum, a suboperculum, and large lateral gulars; the suboperculum may be secondarily lost. The roofing bones of the oticooccipital moiety of the skull consist of medial postparietals flanked laterally by supratemporals anteriorly and tabulars posteriorly. The supraorbital canal primitively may extend as far posteriorly as the transverse otic pit line, but secondarily does not extend into the postparietal. The otic canal may be carried between postparietal and supratemporal or within the supratemporal but always extends into the tabular. Secondarily, the supratemporal may be reduced or lost. The palate primitively articulates with the ethmoid region anteriorly and to basipterygoid and antotic processes of the ethmosphenoid moieity posteriorly; the basipterygoid process may be secondarily lost. The lower jaw consists of a dentary and infradentary (splenial) anterolaterally, followed by a large angular posteriorly; the mandibular canal being borne by infradentary and angular. Mesially there is a series of coronoids dorsal to the dentary and the large prearticular, the most posterior of which is elevated considerably above the occlusal margin of the jaw and occludes lateral to the posterior end of the ectopterygoid. There are separate retroarticular and articular ossifications in Meckel's cartilage that tend to fuse with growth; the lateral surface of the retroarticular is exposed on the posterolateral corner of the lower jaw, may primitively be ornamented and may primitively possibly bear the posterior end of the mandibular lateral line canal. There

are many sclerotics. Postcranially, the wall of the swim bladder is primitively ossified. Neural and haemal arches and spines fuse into median structures. The biserial anal fin is primitively supported proximally by a single element ventral to and braced by the first haemal spines, but seecondarily the basal support becomes free in the ventral body wall anterior to the end of the peritoneal cavity. The distal support of the anal fin consists of a series of axial radials. The serial first dorsal fin rays articulate with a single basal plate lying above the neural spines. The biserial second dorsal fin is supported distally by axial elements and proximally by a single dorsal plate, the stem of which is intercalated between neural spines. The second dorsal plate may secondarily bear an articular facet posterodorsally and anterodorsal processes above the neural spines. The caudal fin is internally and externally structurally symmetrical, the serial fin rays being supported by single series of epichordal and hypochordal basal elements, and there is a terminal axial lobe with a terminal tuft of fin rays unsupported by endoskeletal elements. Fin rays are all unbranched, may be primitively ornamented, are not separated by webbing in the first dorsal fin, and primitively occur in 2:1 ratio to endoskeletal supports in the caudal fins. The caudal fin ray : endoskeletal support ratio may secondarily be reduced to 1:1. Scales are cycloid, deeply overlapping, and ornamented by lines or tubercles on the posterior field. External bones of the skull are all ornamented with lines or tubercles that may be secondarily reduced. There is no cosmine, maxilla or submandibular series.

There are several extant schemes of classification that reflect different attempts to relate the coelacanths to the remainder of the Osteichthyes. The modern classical classification incorporates the Coelacanthiformes (Actinistia) and a coordinate group, the Rhipidistia, within the Crossopterygii (Romer, 1966), isolating the coelacanths from the crossopterygians on the one hand, and actinopterygians and dipnoans on the other. A second scheme involves the supergroup Sarcopterygii, which includes dipnoans, choanata (=rhipidistia), and Coelacanthiformes, as a coordinate category distinct from the Actinopterygii (Miles, 1977). Andrews (1973) has treated the Crossopterygii as distinct from Dipnoi and Actinopterygii, indicating that a division into Actinistia and Rhipidistia does not reflect the continuous nature of character transformations now known, and has suggested the terms Quadrostia and Binostia to include Osteolepiformes, Rhizodonti-

formes, and Onychodontiformes as opposed to Porolepiformes and Coelacanthiformes. New information from the Bear Gulch coelacanths has established that the skull table did indeed evolve separately in Porolepiformes and Coelacanthiformes, both possibly from the type X skull table of Andrews (1973). The type X skull table is also primitive for Actinopterygii, except that the extratemporal is presently unknown in either coelacanths or actinopterygians.

The Bear Gulch coelacanths make it possible to refine conceptions of the primitive states and character transformations within the order, and this information and new information on the Paleozoic Actinopterygii provide an opportunity to reexamine the interrelationships of the Osteichthyes.

OSTEICHTHYAN INTERRELATIONSHIPS

Several critical assumptions must be made in any judgement of interrelationships, especially one in which the evidence is as scanty and as subject to differing interpretations as is the case here. The first and most sweeping is that there is no derived relationship between Dipnoi and Holocephali, as discussed in part by Miles (1977; see Lund, 1977). Also assumed, and discussed above, are that the absences of a maxilla, a submandibular series, and branchiostegal rays are secondary characters, whereas the absence of choanae among the osteichthyans is a primitive feature; further, that the intracranial joint arose but once and was secondarily modified in Coelacanthiformes. It is also assumed, by reference to the Chondrichthyes (Lund, in press) that a baseostaxonost supporting skeleton for the median fins, including the caudal fin, is primitive. Neither the chondrichthyan nor acanthodian conditions, however, are relevant to the present discussion. It is unfortunate, furthermore, that the term "mosaic of snout bones" has to be used, for it carries very little information aside from the observation that there were many, relatively unintelligible, tightly fitting elements.

Comparison of actinopterygians to other Osteichthyes reveals that all other osteichthyans (Sarcopterygii) are derived relative to cheek bone reduction, completeness of the preopercular canal, completeness of the prespiracular series of bones, condition of the opercular-branchiostegal series, and the state of fusion of the neural elements of the axial skeleton (Table 8). Actinopterygians share no derived characters in common with dipnoans. They do share the skull table pattern at the posterior end of the brain-

case with all "crossopterygians" and the reduction in numbers of longitudinal skull bone series to two with the "rhipidistians." The skull table pattern has demonstrably been arrived at in parallel within Dipnoi, and skull roof patterns during the evolution of the actinopterygians has converged upon or approximated even the porolepoid pattern, leading to the caution that this character is subject to convergence. The reduction of numbers of longitudinal series can be demonstrated to occur within dipnoans as well as within coelacanths, and is therefore also relatively unreliable. The assumptions based upon caudal structure and symmetry, however, suggest the independent evolution of the heterocercal caudal fin among several groups. This set of assumptions can only be tested by further study of the internal structure of the skeletons. The Actinopterygii are therefore considered the primitive collateral group of all other Osteichthyes, a grouping to which the term Sareopterygii has been applied (Romer, 1966) (Fig. 77).

The dipnoans are primitive in the multiple series of endoskeletal supports for the caudal fin, a character that needs more data. They share primitively with Actinopterygii the greater posterior extent of the supraorbital canal, the absence of an intracranial joint, and the supraneural-baseost-axonost character of dorsal and anal fin supports (Table 8). They share with all Crossopterygii the derived conditions of the cheek bones, where they are closest to the Porolepiformes primitively, the course of the lateral line canals of the cheek, the specializations of median and lateral gulars, the fused neural arches and spines, similar reductions of the prespiracular series of bones (although they represent an extreme among this group), and the presence of cosmine. Other characters not given in Table 8 but possibly pertinent here are the common possession of two dorsal fins in contrast to the single dorsal of primitive Actinopterygii, and the mutual tendency among porolepoids, osteolepoids and dipnoans to fuse the rostral area into a solid unit. The dipnoans share with coelacanths only the absence of a maxilla and reduction of the branchiostegal series. The dipnoans seem to share sufficient derived characters with all other osteichthyan groups but the actinopterygians to justify the term Sarcopterygii.

The coelacanths are primitive among Crossopterygii, and the remainder of the crossopterygians derived, in the presence of an antorbital commissure, the number of bone series in the anterior part of the skull roof, the separation of the premaxillae

Table 8.—*Comparisons of character states among the Osteichthyan groups. Abbreviations: Actin., Actinopterygii; Coel., coelacanthiformes; Onych., Onychodontiformes; Osteol., Osteolepiformes; Poro., Porolepiformes; P, primitive; D^{1-n}, derived character states one through n, usually implying a continuum; D^9, separately derived state. See text for discussion of characters.*

Character	Actin.	Dipnoi	Coel.	Onych.	Poro.	Osteol.
Supraorbital canal to skull rear	P	P	D^1	D^1	D^1	D
Antorbital commissure	D	P	P	D	D	D
3 longitudinal bone series	D	P	P	D	D	D
2 series posterior to orbit	D^1	P	D^1	D^1	D^2	D^1
Rostral between premaxilla	P	—	P	D	D	D
Anterolateral rostrals	P	—	P	P	D	D
"Mosaic" snout bones	D	P	P	P	P	D
Premaxilla	P	—	P	—	D^9	D^9
Cheek bones (many-few)	P	D^1	D^3	D^2	D^1	D^3
Complete preopercular canal	P	D	D	D	D	D
Preopercular canal bones	D?	P	D^1	D	D	D^1
Prespiracular series	P	D^9	D	D	D	D^1
Infradentaries	D^9	P	D^1	D	D	D
Maxilla	P	D	D	P	P	P
Branchiostegal series	P	D^1	D^2	D	D	D
Submandibular series	D	P	D	P	P	P
Intracranial joint	P	P	D^2	P	D^1	D^1
Choanae, internal	P	P	P	P	D	D
Interclavicles	D	P	D	P	P	P
Anal fin support, proximal	P	P	D	—	D	D
Anal fin support, distal	P	P	D	—	D^2	D
Neural arch-spine	P	D	D	—	D	D
First dorsal support, proximal	P	P	D	—	D	D
First dorsal support, distal	P	P	D^2		D^1	D^1
Second dorsal support, proximal	—	P	D^2	?	D^9	D^1
Second dorsal support, distal	—	P	D^2	?	D^1	D^1
Caudal fin symmetry	D	P	P	P	D	D
Cosmine	P	D	?	D	D	D

by the rostral and lack of a lateral line canal, and the absence of cosmine. Alternatively, however, the coelacanths show potential derivation from a sarcopterygian state in the presence of lateral gulars and absence of a median gular and branchiostegals, from all rhipidistians in the loss of a maxilla with retention of the basic character of the neighboring bones, and in the presence of at least one infradentary. The coelacanths also share with osteolepoids, very similar preopercular canal bones and quadratojugal, characters that could be derived through reduction either from porolepoid or onychodontoid states. They share with all known Crossopterygii the unique dorsal and anal fin supports, although they are further derived in the condition of the first dorsal support. They can be counted as primitive among Crossopterygii in the structural symmetry of caudal fin endoskeleton, possibly sharing this position with the Onychodontiformes.

The osteolepiform and porolepiform fish, called choanates, share derived conditions of the anterolateral rostral area and anterior infraorbital canal, the position of the premaxillae and rostral, the presence of choanae, and the structure and symmetry of the caudal fin.

There are, therefore, several alternative schemes of interrelationships of the Osteichthyes under the above assumptions, depending upon the emphasis placed upon character derivations that are almost all losses or reductions. The actinopterygians are less closely related to other osteichthyans than they are to each other, leading to the suggestion of a primary binary division into Actinopterygii and Sarcopterygii. Within the Sarcopterygii, if one chooses to emphasize the significance of the relationship between choanates, as seems to us to be the most parsimonious choice based upon the least number of possible parallelisms, a scheme as in Fig. 77B suggests itself. If, however, it is assumed that among other elements the coelacanths have lost are the internal choanae and a flexible air bladder, there are several derived resemblances between Coelacanthiformes

and Osteolepiformes that can be emphasized, as in Fig. 77A. Either scheme fails adequately to take into consideration that the coelacanths are unique among a spectrum of related groups. The terms rhipidistia and actinistia in particular imply separate derivation of the two from a common stock, an idea that can no longer be justified.

CLASSIFICATION

The broad systematic conclusions of this paper can be summarized in an outline classification.

Class Osteichthyes
    Subclass Actinopterygii
    Subclass Sarcopterygii
        Infraclass Dipnoi
        Infraclass Crossopterygii
            Superorder Achoana
                Order Onychodontiformes
                Order Coelacanthiformes
                    Suborder Hadronectoroidei
                        Family Hadronectoridae
                    Suborder Coelacanthoidei
                        Family Diplocercidae
                        Family Rhabdodermatidae
                        Family Coelacanthidae
                        Family Laugiidae
              Superorder Choanata
                Order Osteolepiformes
                Order Rhizodontiformes
                Order Porolepiformes

FUNCTIONAL RELATIONSHIPS

Point by point analysis of characters, with the aim of understanding interrelationships of groups, negates, obscures, or ignores the functional integration of the characters that in their totality render the groups separate biological entities with unique adaptive pathways. The Coelacanthiformes incorporate a large number of cranial characters into a feeding mechanism quite distinctive in function from the groups of fish with which it can be related as well as from any other group of Paleozoic fish. The postcranial characters are also summed up in a particular propulsive mechanism with distinctive characteristics relative to the other members of Paleozoic ichthyofaunas. Without detailed exposition of the functions of the basal osteichthyan groups, a short summary of contrasting conditions may be helpful to an understanding of the coelacanth adaptive pathway.

The basic feeding mechanism of all coelacanths
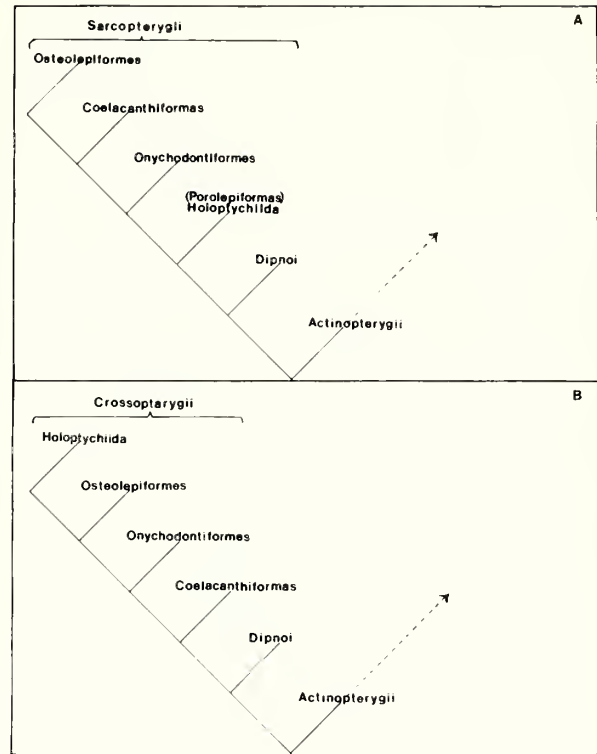
Fig. 77.—Alternative schemes of Osteichthyan interrelationships. See text for explanation.

involves suction, rather than delivery of power to the bite as in other Crossopterygii and primitive Actinopterygii (Lund et al., in press). The leverage arrangements of the palate-braincase articulation produced by the antotic process (Thomson, 1970) of coelacanths decouples the jaw and anterior moiety of the braincase, compared to the arrangement of the crossopterygian feeding mechanism. Restriction of the gape by a high coronoid, rather than by shortening the jaw as in teleosts, produces not more power delivered to a bite that lacks teeth in almost all coelacanths, but a nozzle with intake diameter restricted and consequent adjustment of intake velocity. The evolution of fleshy lips with maintenance of a long lower jaw may be seen to serve several functions, channeling and restriction of water flow in respect to the aperture and to timing of opening of the mouth, and restriction of the direction of water flow in the event of large mouth opening. The absence of strong biting forces delivered to the anterior part of the braincase can be related in turn to several different developments within coelacanths, such as the lack of consolidation of external bones

into a solid unit or tightly knit mosaic to brace against the lower jaw, the absence of a maxilla, the reduction of the dentary, and reduction of ossification in the ethmosphenoid moiety of the braincase. Reduction of the opercular series and decoupling of the gulars from the operculum, backward extension of the soft opercular flap, freeing of the shoulder girdle from the braincase dorsally and an increasingly mobile interrelationship of shoulder girdle elements, the development of cervical vertebrae, and repeated tendencies to articulate the operculum (hyoid and operculum?) directly with the posteriormost corner of the braincase, can all be correlated with intracranial involvement in the operation of the opercular-branchial pump, as distinct from the palatal suction pump (Lund et al., in press). Thus, while the coelacanths share with other crossopterygians an intracranial joint that undoubtedly indicates a close morphogenetic and phylogenetic relationship, they have diverged from the ancestral stock along a quite unique adaptive line in terms of feeding mechanism. They are far removed indeed from either the autostylic, well braced dipnoans or the actinopterygian adaptation for speedy closure of the mouth with a firm bite.

The coelacanth postcranial skeleton, consisting of lobed paired and median fins (except the first dorsal fin) and a broadly expanded caudal fin with individual endoskeletal supports for both epichordal and hypochordal components, corresponds closely to that of other crossopterygians as well as to dipnoans. These fish can all be broadly characterized as having high drag bodies with tails of low aspect ratio, indicative of potentially high acceleration but low sustainable cruising speed (Dicanzio, in press). The mobility and positions of the median and paired fins would confer high ability to maneuver, as would characterize lurking predators or slow cruising feeders (Andrews and Westoll, 1970a; Keast and Webb, 1966). In this regard, the coelacanths differ the least from the Onychodontiformes, the crossopterygian group most distinct from them in feeding adaptations. The actinopterygian body form contrasts sharply with that of all sarcopterygians in having a relatively low drag profile and in having higher caudal aspect ratios; the former condition resulting from the single dorsal fin, the lack of fleshy extensions and the generally compressed body and the latter condition made possible by the heterocercal tail. Lurking predators among the actinopterygians tend to have rounded caudal outlines, rounder body cross sections and even in the Bear Gulch, lobed pectoral fins (Keast and Webb, 1966; Dicanzio, in press; Lowney, 1980; Andrews and Westoll, 1970a).

ACKNOWLEDGMENTS

LITERATURE CITED

AGASSIZ, L. 1837–1843. Rercherches sur les poissons fossiles. Neuchatel, 1,420 pp.

ALEXANDER, R. M. 1973. The chordates. Cambridge Univ. Press, London, 480 pp.

ANDREWS, S. M. 1973. Interrelationships of crossopterygians. Pp. 138–177, in Interrelationships of fishes (P. H. Greenwood, R. S. Miles, and C. Patterson, eds.), Zool. J. Linn. Soc., Suppl. 1.

———. 1977. The axial skeleton of the coelacanth, Latimeria. Pp. 277–288, in Problems in vertebrate evolution, Linn. Soc. Symposium Ser., 4.

ANDREWS, S. M., and T. S. WESTOLL. 1970a. The postcranial skeleton of Eusthenopteron foordi (Whiteaves). Trans. Roy. Soc. Edinburgh, 68:207–329.

———. 1970b. The postcranial skeleton of rhipidistian fishes excluding Eusthenopteron. Trans. Roy. Soc. Edinburgh, 68: 391–489.

BAIRD, D. 1955. Latex micro-molding and latex-plaster molding mixture. Science, 122:202.

BERG, L. S. 1958. System der rezenten und fossilen fischartigen und fische. VEB Deutscher Verl. d, Wissensch., Berlin, 310 pp.

BERNACSEK, G. M. 1977. A lungfish cranium from the Middle Devonian of the Yukon Territory, Canada. Palaeont. (Abt. A), 157:175–200.

BJERRING, H. C. 1973. Relationships of Coelacanthiformes. Pp. 179–205, in Interrelationships of fishes (P. H. Greenwood, R. S. Miles, and C. Patterson, eds.), Zool. J. Linn. Soc., Suppl. 1, 53.

DENISON, R. H. 1968. The evolutionary significance of the ear-

liest known lungfish, *Uranolophus*. Nobel Symposium, 4: 247–257.

DICANZIO, J. A. In press. Ecomorphology of the Osteichthyes from the Bear Gulch Limestone. Comptes Rendus, IX Int. Cong. Carboniferous Stratigraphy and Geology, Urbana, Illinois.

EASTMAN, C. R. 1908. Notice of a new coelacanth from the Iowa Kinderhook. J. Geol., 16:357–362.

ECHOLS, J. 1963. A new genus of Pennsylvanian fish (Crossopterygii, Coelacanthiformes) from Kansas. Univ. Kansas Publ., Mus. Nat. Hist., 12:475–501.

FOREY, P. L. 1981. The coelacanth *Rhabdoderma* in the British Isles. Palaeontology, 24:203–229.

FREIHOFER, W. C. 1978. Cranial nerves of a percoid fish *Polycentrus schomburghii* (Family Nandidae), a contribution to the morphology and classification of the order Perciformes. Occas. Papers California Acad. Sci., 128:1–78.

GARDINER, B. 1963. Certain palaeoniscoid fishes and the evolution of the snout in actinopterygians. Bull. British Mus. (Nat. Hist.), Geol., 8:255–325.

GATZ, A. J., JR. 1979. Community organization in fishes as indicated by morphological features. Ecology, 60:711–718.

GOODRICH, E. S. 1930. Studies on the structure and development of vertebrates. MacMillan, London, 837 pp.

GREENWOOD, P. H., D. E. ROSEN, S. H. WEITZMAN, and G. S. MYERS. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bull. Am. Mus. Nat. Hist., 131:359–456.

GRIFFITH, R. W., and K. S. THOMSON. 1973. *Latimeria chalumnae*: reproduction and conservation. Nature, 242:617–618.

HORNER, J. R., and R. LUND. In press. Biotic distribution and diversity in the Bear Gulch Limestone of central Montana. Comptes Rendus, Ninth Int. Cong. Carboniferous Stratigraphy and Geology, Urbana, Illinois.

HUXLEY, T. H. 1866. Illustrations of the structure of the crossopterygian ganoids. Mem. Geol. Surv. United Kingdom, 12:1–44.

JARVIK, E. 1942. On the structure of the snout of crossopterygians and lower gnathostomes in general. Zoo. Bidrag från Uppsala, 21:295–675.

———. 1948. On the morphology and taxonomy of the Middle Devonian osteolepid fishes. Kungl. Svenska Vetenskapsakad. Handl., (3) 25:1–301.

———. 1954. On the visceral skeleton in *Eusthenopteron* with a discussion of the parasphenoid and palatoquadrate in fishes. Kungl. Svenska Vetenskapsakad. Handl., (4) 5:1–104.

———. 1963. The composition of the intermandibular division of the head in fish and tetrapods and the diphyletic origin of the tetrapod tongue. Kungl. Svenska Vetenskapsakad. Handl., (4) 9:1–74.

———. 1972. Middle and Upper Devonian Porolepiformes from East Greenland with special reference to *Glyptolepis groenlandica* n. sp. and a discussion on the structure of the head in Porolepiformes. Meddel. om Grønland, 187:1–307.

JESSEN, H. 1973. Weitere fischreste aus dem oberen plattenkalke der Bergisch-Gladbach Paffrather mulde (Oberdevon, Rheinisches Schiefergebirge). Palaeontographica (Abt. A), 143:159–187.

JOLLIE, M. 1980. Development of head and pectoral girdle skeleton and scales in *Acipenser*. Copeia, pp. 226–227.

KEAST, J. A., and D. WEBB. 1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. J. Fish. Res. Bd. Canada, 23:1835–1874.

KOLLAR, E. J. 1978. The role of collagen during tooth morphogenesis—some genetic information. Pp. 1–11, *in* Development, function and evolution of teeth (Butler and Joysey), Academic Press.

LEHMAN, J. P. 1952. Etude complémentaire des poissons de l'Eotrias de Madagascar. Kungl. Svenska Vetenskapsakad. Handl., (4) 2:1–201.

LOWNEY, K. A. 1980. A revision of the family Haplolepidae (Actinopterygii, Paleonisciformes) from Linton, Ohio (Westphalian D, Pennsylvanian). J. Paleont., 54:942–953.

———. In press. The Palaeonisciformes from the Bear Gulch Limestone. Comptes Rendus, IX Int. Cong. Carboniferous Stratigraphy and Geology, Urbana, Illinois.

LUMSDEN, G. I., W. TULLOCH, M. F. HOWELLS, and A. DAVIES. 1967. The geology of the neighborhood of Langholm. Mem. Geol. Survey Scotland, Edinburgh, 255 pp.

LUND, R. 1977. New information on the evolution of the bradyodont Chondrichthyes. Fieldiana, Geol., 33:521–539.

———. 1980. Viviparity and intrauterine feeding in a new holocephalan fish from the Lower Carboniferous of Montana. Science, 209:697–699.

———. In press. Ecomorphology of the Bear Gulch Chondrichthyes. Comptes Rendus IX Int. Congr. Carboniferous Stratigraphy and Geology, Urbana, Illinois.

LUND, R., and W. L. LUND. 1984. New genera and species of coelacanths from the Bear Gulch Limestone (Lower Carboniferous) of Montana (U.S.A.). Geobios, 17, fasc. 2:237–244.

LUND, W. L., R. LUND, and G. KLEIN. In press. Coelacanth feeding mechanisms and the ecology of the Bear Gulch coelacanths. Comptes Rendus, IX Int. Cong. Carboniferous Stratigraphy and Geology, Urbana, Illinois.

MELTON, W. G., JR. 1969. A new dorypterid fish from central Montana. Northwest Sci., 43:196–206.

MILES, R. S. 1973. Articulated acanthodian fishes from the Old Red Sandstone of England, with a review of the structure of the acanthodian shoulder girdle. Bull. British Mus. (Nat. Hist.), Geol., 24:111–213.

———. 1977. Dipnoan (lungfish) skulls and the relationships of the group: a study based on new species from the Devonian of Australia. Zool. J. Linn. Soc. 61:1–328.

MILLOT, J., and J. ANTHONY. 1958. Anatomie de *Latimeria chalumnae* 1. Squelette, muscles et formations de soutien. Centre National de la Recherche Scientifique, Paris, 122 pp.

MOY-THOMAS, J. A. 1935. A synopsis of the coelacanth fishes of the Yorkshire coal measures. Ann. Mag. Nat. Hist., (10), 15:37–46.

———. 1937. The Carboniferous coelacanth fishes of Great Britain and Ireland. Proc. Zool. Soc., B (3):383–415.

MOY-THOMAS, J. A., and T. S. WESTOLL. 1935. On the Permian coelacanth, *Coelacanthus granulatus* Ag. Geol. Mag., 72: 446–457.

MOY-THOMAS, J. A., and R. S. MILES. 1971. Palaeozoic fishes. Saunders, Philadelphia, 259 pp.

NEWBERRY, J. S. 1856. Descriptions of several genera and species of fossil fish from Carboniferous strata of Ohio. Proc. Acad. Nat. Sci. Philadelphia, 8:96–100.

———. 1873. Report of the Geological Survey of Ohio. Paleontology. Description of fossil fishes. 1 (2):247–358.

NYBELIN, O. 1956. Les canaux sensoriels de museau chez *Elops saurus*. Ark. Zool., (2) 10:453–458.

———. 1967. Notes on the reduction of the sensory canal sys-

tem and of the canal bearing bones in the snout of higher actinopterygian fishes. Ark. Zool., (19) 2:235–246.

OBRUCHEV, D. V. 1967. Fundamentals of Paleontology, XI: Agnatha, Pisces. Israel Prog. Sci. Transl., Jerusalem, 825 pp.

OLSEN, P., and P. M. GALTON. 1977. Triassic-Jurassic tetrapod extinctions; are they real? Science, 197:983–986.

ØRVIG, T. 1975. Description, with special reference to the dermal skeleton, of a new radotinid arthrodire from the Gedinnian of Arctic Canada. Coll. Inter. C.N.R.S., 218:41–71.

PARRINGTON, F. R. 1949. A theory of the relations of lateral line canals to dermal bones. Proc. Zool. Soc. London, 119: 65–78.

PATTERSON, C. 1965. The phylogeny of the Chimaeroids. Phil. Trans. Roy. Soc. London, B, 249 (757):101–219.

PATTERSON, C., and D. E. ROSEN. 1977. Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. Bull. Amer. Mus. Nat. Hist., 158:81–172.

PEHRSON, T. 1947. Some new interpretations of the skull in Polypterus. Acta Zool., 28:400–455.

POPLIN, C. 1973. Survivance de la "ligne epibranchiale" en particular du "canal dorso-lateral-antérieur" (ligne profonde) chez les vertèbres inférieurs. Bull. Mus. d'Hist. Nat., Paris, 175:117–140.

REIS, O. M. 1888. Die coelacanthien. Palaeontographica, 35: 1–94.

RICHARDSON, E. S., and R. G. JOHNSON. 1971. The Mazon Creek faunas. Proc. N. Amer. Paleo. Convention, 1:1222–1235.

ROMER, A. S. 1966. Vertebrate paleontology. Univ. Chicago Press, 3rd ed., 468 pp.

ROSEN, D. E., P. FOREY, B. G. GARDINER, and C. PATTERSON. 1981. Lungfishes, tetrapods, paleontology and plesiomorphy. Bull. Amer. Mus. Nat. Hist., 167:159–276.

SÄVE-SÖDERBERGH, G. 1941. Notes on the dermal bones of the head in Osteolepis macrolepidotus Ag. and the interpretation of the lateral line system in certain primitive vertebrates. Zool. Bidrag från Uppsala, 20:523–542.

SCHAEFFER, B. 1941. A revision of Coelacanthus newarki and notes on the evolution of the girdles and basal plates of the median fins in the Coelacanthini. Amer. Mus. Novitates, 1110:1–17.

———. 1952. The Triassic coelacanth fish Diplurus, with observations on the evolution of the Coelacanthini. Bull. Amer. Mus. Nat. Hist., 991:29–78.

———. 1962. A coelacanth fish from the Upper Devonian of Ohio. Sci. Publ. Cleveland Mus. Nat. Hist. 1:1–14.

———. 1967. Late Triassic fishes from the western United States. Bull. Amer. Mus. Nat. Hist., 135:285–342.

SCHAUMBERG, G. 1978. Neubeschribung von Coelacanthus granulatus Agassiz (Actinistia, Pisces) aus dem Kupferschiefer von Richelsdorf (Perm, W.-Deutschland). Palaeont., 52: 169–197.

SCHOENER, T. W. 1974. Resource partitioning in ecological communities. Science, 185:27–39.

SCHRAM, F. 1976. Crustacean assemblage from the Pennsylvanian Linton vertebrate beds of Ohio. Palaeontology, 19: 411–412.

SCHRAM, F., and J. R. HORNER. 1978. Crustacea of the Mississippian Bear Gulch Limestone of central Montana. J. Paleont., 52:394–406.

SCHULTZE, H.-P. 1972. Early growth stages in coelacanth fishes. Nature, 236:90–91.

———. 1973. Crossopterygier mit heterozerker schwanzflosse

aus dem Oberdevon Kanadas. Palaeontographica, (Abt. A), 143:188–208.

———. 1979. Growth and spawning places of Rhabdoderma (Pisces, Osteichthyes) in Pennsylvanian deposits of Illinois, U.S.A. Abstracts IX Int. Congr. of Carboniferous Strat. Geol., 198.

SCOTT, H. W. 1973. New Conodontochordata from the Bear Gulch Limestone (Namurian, Montana). Publ. Mus. Miehigan State Univ., Paleontology, 1:81–100.

SMITH, C. L., C. S. RAND, B. SCHAEFFER, and J. W. ATZ. 1975. Latimeria, the living coelacanth, is ovoviviparous. Science, 190:1105–1106.

STENSIÖ, E. A. 1921. Triassic fishes from Spitzbergen, Pt. 1. Holhausen, Vienna, 307 pp.

———. 1922. Uber zwei Coelacanthiden aus dem Oberdevon von Wildungen. Palaont. Z., 4:167–210.

———. 1937. On the Devonian coelacanthids of Germany with special reference to the dermala skeleton. Kungl. Svenska Vetenskapsakad. Handl., (3) 16:1–56.

———. 1947. The sensory lines and dermal bones of the cheek in fishes and amphibians. Kungl. Svenska Vetenskapsakad. Handl., (3) 24:1–195.

TAVERNE, L. 1977. Ostéologie, phylogénèse et systematique des Téléostéens fossiles et actuels du superordre des Ostéoglossomorphs. Acad. R. Belg. Mem. Classe Sci., (2) 17:1–235.

THOMSON, K. S. 1969. The biology of the lobe-finned fishes. Biological Rev., 44:91–154.

———. 1970. Intracranial movement in the coelacanth Latimeria chalumnae Smith (Osteichthyes, Crossopterygii). Postilla, 148:1–12.

THOMSON, K. S., and K. S. W. CAMPBELL. 1971. The structure and relationships of the primitive Devonian lungfish Dipnorhynchus sussmilchii (Etheridge). Bull. Peabody Mus. Nat. Hist., 38:1–109.

TRAQUAIR, R. H. 1881. Report on fossil fishes collected by the Geological Survey of Scotland in Eskdale and Liddlesdale. Pt. I. Ganoidei. Trans. Roy. Soc. Edinburgh, 30:15–71.

———. 1905. Notes on the Lower Carboniferous fish of eastern Fifeshire. Proc. Roy. Phys. Soc. Edinburgh, 14:80–86.

WATSON, D. M. S. 1921. On the coelacanth fish. Ann. Mag. Nat. Hist., (9) 8:320–337.

———. 1925. The structure of certain palaeoniseids and the relationships of that group with other bony fish. Proc. Zool. Soc. London, pp. 815–870.

WENZ, S. 1975. Un nouveau coelacanthidé du Crétacé inférieur du Niger, remarques sur la fusion des os dermiques. Coll. Intern. C. N. R. S., 218:175–190.

WESTOLL, T. S. 1939. On Spermatodus pustulosus Cope, a coelacanth from the "Permian" of Texas. Amer. Mus. Novitates, 1017:1–23.

———. 1949. On the evolution of the Dipnoi. Pp. 121–184, in Genetics, paleontology and evolution (G. L. Jepsen, E. Mayr, and G. G. Simpson, eds.), Princeton Univ. Press, Princeton, New Jersey.

WILLIAMS, L. A. 1981. The sedimentational history of the Bear Gulch Limestone (Middle Carboniferous, Central Montana). Unpublished Ph.D. dissertation, Princeton Univ., 242 pp.

WOURMS, J. P. 1977. Reproduction and development in chondrichthyan fishes. Amer. Zool., 17:379–410.

ZIDEK, J. 1976. Kansas Hamilton Quarry (Upper Pennsylvanian) Acanthodes, with remarks on the previously reported North American occurrenees of the genus. Univ. Kansas Paleont. Contrib., 83:1–40.